Conspecific Community Dynamics Models and their applications

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CONTENTS

Abstract

The thesis introduces a new integrated approach to ecological and evolutionary modeling, the goal of which is to create an analytical platform for applied interdisciplinary researches.

This Conspecific Community Dynamics Model (CCDM) approach establishes links between the ecology of the individual, community ecology, behavioral ecology, population dynamics and natural selection. The approach related to co-selection timescale and single-species (conspecific) community scale. The co-selection timescale extends from several to several hundreds of generations. Presumably, at this timescale, viable mutations leading to a change in the underlying physiology of the species do not occur, but the interaction between individuals within a conspecific community can lead to a change in the frequency distribution of certain functional traits. The conspecific community scale is an organizational scale, which is intermediate between entire population and the individual. This is the scale on which an organism can be recognized not only as a representative of their own species, not only as a passive carrier of genetic material, but also as a member of the conspecific community in which its reproductive success depends on other members of this community. This is the scale on which the differences between the two conspecific communities can potentially undergo a critical transition and becomes differences between species, and thus, this scale may occur at the earliest stages of reproductive isolation. Finally, this is the scale at which apparently random differences between individuals are added to the overall mosaic of an intrinsically organized system.

This approach emphasizes that the phenomenon of single-species organisms within a population organizing themselves into conspecific communities has deep natural reasons and cannot be ignored; furthermore, this fact may become a key nodal point of the synthesis of ecology and evolution. The approach also stresses that such synthesis can hardly be realized at the level of mechanical combinations of existing models, but requires a special analytical platform that would (i) include the basic postulates of population ecology, quantitative genetics and evolutionary biology, (ii) allow, despite the inherent stochasticity, the investigation of conspecific communities at the level of cause-effect relationships.

Half of the thesis relates to the basic issues associated with the mathematical formalization of the approach, the other half is entirely devoted to its various applications in the fields of demography, fish population dynamics, community ecology, microbiology and community epidemiology. For each of these fields a set of CCDM models are constructed, subsequent analyses of which lead to interesting results. These results are intended to demonstrate the great potential of this approach, its ability to integrate various aspects of the population and its analytical power.

It should be emphasized that this approach does not create any new entities, but is instead based on the widely-accepted (within each particular field) postulates. Nevertheless, the consideration of these postulates in combination sometimes leads to much unexpected results. However, the distinguishing feature of the approach is its analyticity, that is, any result that at first glance seems unusual, can be traced to these basic tenets.

LIST OF PAPERS

The thesis is based on the following five papers, which are referred to by their Roman numerals.

Paper I	Sadykov A. M., (2010), Conspecific community dynamics.
Paper II	Sadykov A. M. and Stenseth Nils Chr., (2009), Rethinking the basis of the population growth.
Paper III	Sadykov A. M. and Stenseth Nils Chr., (2010), Shoal-based approach to the fish population dynamics.
Paper VI	Sadykov A. M. and Stenseth Nils Chr., (2009), Epidemiology of conspecific community.
Paper V	Sadykov A. M. and Stenseth Nils Chr., (2009), Modeling the interactions between conspecific communities.

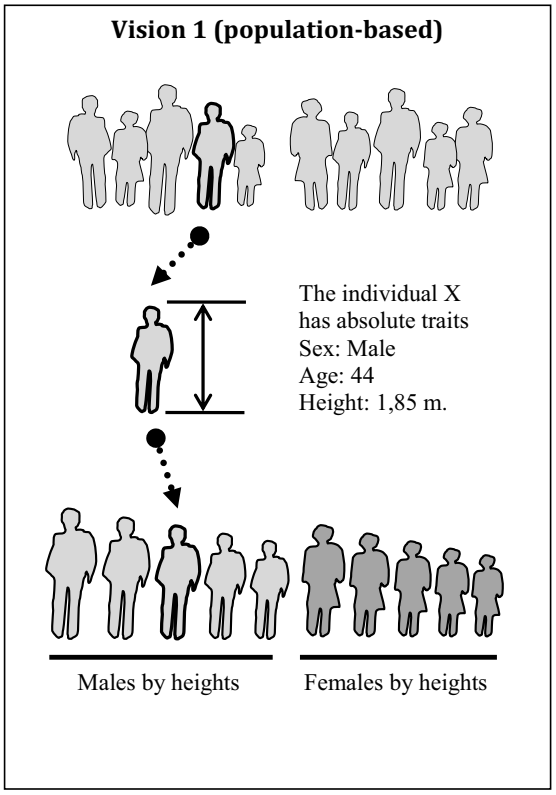
Preface

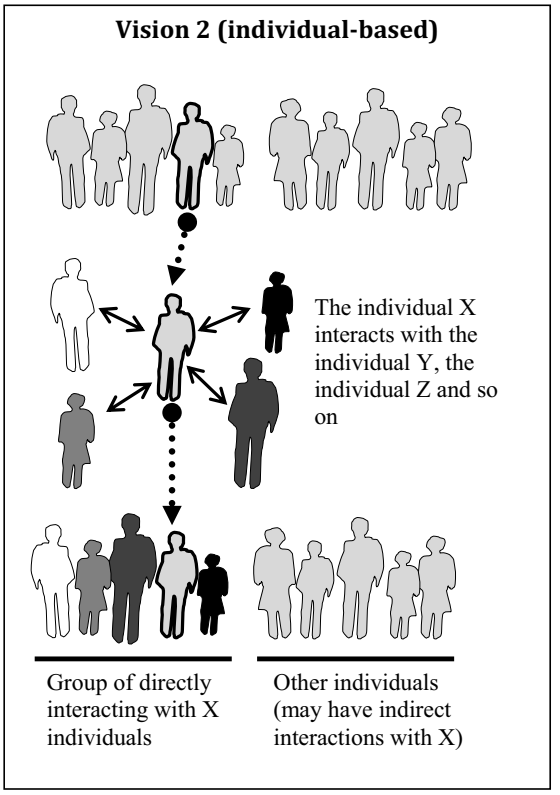
Human life is very short, but the life of a scientist is even shorter, we cannot afford to do researches that do not lead to new results.
Lev. D. Landau

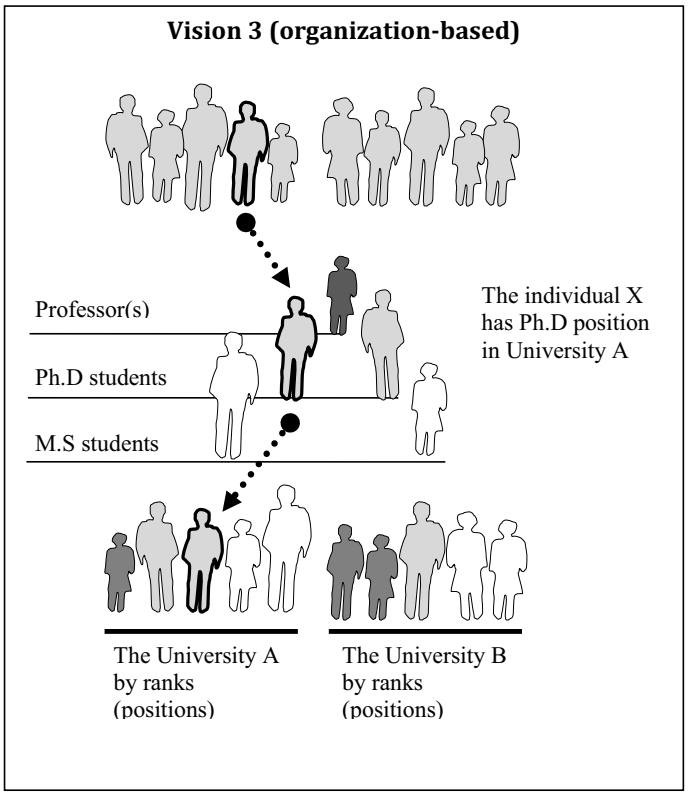
99% of all new research results in the end turn out to be rubbish, but the remaining 1% that is the raison d'être of science.
Anonymous

I am writing this preface, because this thesis involves a look at population and population processes, which is not common in current biological literature, at least in context of population dynamics. Here, I will try to explain the essence of this research, using highly informal examples from everyday-life. Main goal of this chapter is to give a simple intuitive understanding of basic principles, rather than strict formal description. I also hope that this chapter will help readers who are not very familiar with this field to get some useful information and perhaps a sense of the hidden beauty of population dynamics.

So, what is this thesis about? Essentially, it is about a special look at the population and about the special *vision* of population processes, which lies at the heart of any approach to population modeling. In order clearly illustrate this point, let me give a simple example. Let us look around; we can see different people around us (see picture 0.1). However, we can have a different vision for them, for example, we may see individuals of different sex, age, height, weight and so on (V*ision 1*) or we may see individuals who have some personal relationship with each other (V*ision 2*), and finally we can see the individuals who occupy certain positions in some organizations or communities (V*ision 3*). Of course, each "vision" only reflects a certain aspect of reality and they are not mutually exclusive. The same individual may have age, height, sex, and also be involved in the personal interaction and be a member of a community. Moreover, it is clear that these different visions are somehow connected to each other, for example, we can expect that individuals in positions of professors are older than the master students or that the interactions between individuals may change with age. However, at the same time, they cannot be reduced to each other, because it was originally based on the different features of the individual. The Vision 1 makes particular accent on *absolute traits* of the individual, whereas the Vision 2 on *personality* and interactions between individuals. The Vision 3 emphasizes *relative traits* of the individual and his or her position within community. Therefore, general question "which one better represents reality?" does not have a lot of sense. However, if we are interested in specific aspects of population processes, one vision may be more revealing than others may. In this thesis I am particularly interested in the distribution of resources among the individuals, in such situation the advantages of the vision 3 are becoming evident. To illustrate this point, let us make the following thought experiment (see picture 0.1): Try to estimate the salary of an individual based on (a) sex, age, height (b) personal connections (c) position in organization. Of course, (a) or Vision 1 and (b) or Vision 2 in some degree can be helpful, but note that (c) or Vision 3 can give an exact number.







Picture 0.1
Looks on the same collection of individuals, each vision makes accent on particular aspect of the individual and as result sees a certain structure of this gathering.
Vision 1 emphasizes an absolute trait(s) of the individual (trait, which can be measured for each individual separately from other individuals) and structures this gathering according to value of absolute trait(s).
Vision 2 emphasizes pair-wise interactions between individuals and structures this gathering by roles that the individual plays in each interaction.
Vision 3 emphasizes a membership of the individual within some organization and structures this gathering by rank or position of the individual within his/her organization or community. Note that trait "be on position" is not absolute one.

Someone might argue that such a sophisticated community or organization can exist only among the higher animals. However, the microbial world also shows numerous examples of self-organized communities. For instance, some species of bacteria can form a biofilms or fractal-like structures in which position of each cell within colony is determined by others cells and crucially affects the individual resource consumption.

At present, Vision 1 (which underlies the classical population modelling) and Vision 2 (which underlies the individual and agent based modelling) totally dominate in the field of population dynamics. However, it is interesting to note that Vision 3, historically, is not new, in fact, Malthus [1798] and especially Condorcet [1794], no matter how different their views are, nonetheless recognized the fundamental role of inequality of resource allocation, which is induced by the organizational structure of the population. Unfortunately, in the field of population dynamics, the ideas of Malthus and Condorcet have not received further comprehensive development. Original ideas of Malthus have been oversimplified to the level of Verhlust's equation; thus, an explicit connection with resources has been lost. Note that the concept of carrying capacity, which implicitly takes into account the need for resources for the *population as a whole*, does not coincide with the postulate of Malthus on the necessary resources for the survival of *each individual*. On the other hand, Condorcet's revolutionary ideas about the evolution of society through natural changes in the structure of resource allocation (individuals who have great opportunities for the resources themselves leave more offspring that leads to the gradual equalization of the inequality),which anticipated an evolutionary thinking long before Darwin, but were overlooked by biologists at all.

Hereafter, I will develop an approach based on the Vision 3, it is not in any way underrate the other approaches. On the contrary, it allows you to look at many of the classical problems of ecology and evolution from a new angle. There will be appropriate to cite an example of how three radically different visions can successfully co-evolve. In physics, the same amount of gas can be considered from the standpoint of thermodynamics, mechanics and statistical mechanics. In the first case, the gas is considered as a single entity that has some overall thermodynamic characteristics. In the second case, the gas is considered as a set of individual interacting particles. In the third case, the gas is seen as a coherent ensemble of particles, in which each particle occupies a definite position within overall energy distribution. Someone can note resemblance between thermodynamics, mechanics and statistical mechanics standpoints from one hand and Vision 1, Vision 2 and Vision 3 from other. In fact, J. Maynard Smith supposed a reformulation of classical population dynamics in form of thermodynamics equations in early 70's, yet Individual-based models have a close tie with Cellular Automata Theory, while methods of statistical physics have been extensively used in evolutionary studies [H.P.de Vladar and N.H.Barton, TREE 2011]. However, until now, using methods of statistical physics in biology was exclusively focused on the dynamics of genotypes; this thesis expands its use on the dynamics of conspecific communities.

Table 1 provides a comparative analysis of three Visions. It clearly shows that a direct comparison of models based on different visions do not seem possible, simply because they are dealing with a different set of basic parameters. It should be noted that such circumstances could lead to terminological confusion. For example, the term "physiologically structured epidemiological model" (Paper IV) can be interpreted differently depending on Vision on which model is based. The key word here – "structured" within the framework of Vision 1, it means that "structured by the absolute trait(s)", respectively, physiology seen in the aspect of sex, age or body-size. In contrast, in Vision 3, a "structured" means "structured by resource consumption of the individual", thus physiology seen in the aspect of nutrition-depended immune response.

Table 1 Basic characteristics of three visions on population			
	VISION 1	VISION 2	VISION 3
Makes accent on	Absolute trait (s) of the individual (trait, which can be measured for each individual separately from other individuals)	Interactions between individuals and unique life-history of each individual	Relative trait(s) of the individual (trait, which can only be measured by comparing individuals with each other)
Defines population as	Arbitrary collection of individuals or some quantity of biomass	Some set of unique interacting individuals	Community of diverse (by their position) members
Considers the individual as	Not essential entity (can be equally imply to biomass), passive carrier of some absolute trait(s)	Essential and unique entity, active decision makers	Essential, but not unique entity, member of some conspecific community
Structures the population by	Absolute trait(s)	Roles in pair-wise interactions (dove-hawk, buyer-seller, child-parent, etc)	Position within community and individual resource consumption
Considers resource(s) as	Implicit factor, which can be indirectly taken into account on population level by introducing an "carrying capacity"	One among many factors, which can affect of the individual life-history	Explicit and essential factor, which defines survival and reproduction of each individual
Evaluates dynamics as	Process(es) going on population level only	Process(es) going on level of the individual only	Two distinct processes(resource obtaining and redistribution on community level and birth-death on the level of the individual)
Considers an inequality between individuals as	Differences in some absolute trait(s)	Differences in roles and (or) personalities	Difference in position within community, which reflects difference(s) in relative trait(s)
Inspired by	Euler's age structured model, Verhlust's interpretation of Malthus views, Lotka-Volterra models	Cellular Automata Theory, Game theory, classical mechanics, microeconomics	Condorcet and partially Malthus views, statistical mechanics, macroeconomics
Underlies	Classical population modelling	Individual based and agent based modelling	Conspecific community modelling
Current stage of development	Stagnation	Booming across several fields	Embryonic
Main empirical evidence	Any physical object always has absolute trait(s)	Individuals are exist and interact	Conspecific communities are exist
Considers behavior of the individual as	Not visible on population level	Individual choice between several alternatives	The window of opportunity, which the individual has according his position

Table 1 Basic characteristics of three visions on population (continuation)			
	VISION 1	VISION 2	VISION 3
Considers personality as	Not existing (everything is determined by absolute trait(s))	Consistency of choice between apparently equivalent alternatives	Potential for changing of position within community
Considers emergent properties (EP) as	Implicitly existing behind of a density-dependence	Not existing at all (EP can be potentially reduced to some combination of absolute trait(s) and individual interactions)	Explicitly existing and irreducible, while density-dependence is overall result of nutrition-dependent physiology
Considers self-organization as	Implicit, but can be anticipated throughout a stability of distribution of absolute trait(s)	One of possible outcome of various pair-wise interactions between individuals	Immanent
Considers effect of stochasticity as	Separable from essentially deterministic underlying mechanism	One of the factor, which may affect individual decision making process	Immanent (separation on deterministic and stochastic components is not possible)
Considers fitness as	Some function of absolute trait(s), hence fitness is essentially absolute property of the individual	Function of role(s) and (or) personality	Function of relative trait(s) and resource consumption of the individual. Note that relative fitness and fitness as function of relative trait(s) are different
Evaluates effect of evolution as	Changing in some absolute trait(s), which in turn can affect survival and (or) reproduction	Changing in some absolute trait(s) and (or) behavior of the individual	Changing in some relative trait(s), which can affect structure of community
Key words	Age, sex, body-size distributions, carrying capacity, density-dependence, partial differential equations	Personality, interactions, individual behavior, life-history, games, computer simulations	Community, intrinsic organization, collective behavior, resource distribution, competiveness, nutrition-dependent physiology

Which of these models had better correspond to reality? The answer to this question depends on the type of pathogen and its relationship with the host immune system. If we consider the susceptibility to the pathogen that depends entirely on the sex, age or body size of the host, then the model is based on Vision 1 will be adequate to reality. On the contrary, if we consider the susceptibility to the pathogen that depends on host nutritional status (starving individuals are easier to contract the infection), then the model is based on Vision 3 is more appropriate. Note that pathogens selectively affecting individuals of a particular sex, age or body size are much less common (if exist at all) than those, which selectively infect individuals with weakened (by malnutrition) immune system. It is not in any way imply that there is no correlation between age, sex or body size, and susceptibility to the pathogen, such

correlations *inevitably exist*, but it is only the reflection of a causal link between the state of the immune system and the ability of the pathogen to overcome it. Unfortunately, models based on Vision 1 are forced to accept such correlations as causality, which eventually leads to major discrepancies with data [Lloyd-Smith, J.O. et al. TREE 2005]. Shortly, main advantage of models based on Vision 3 is its ability to take into account nutrition-depended immune system response explicitly, which in turn allows reaching a new level of understanding in the study of epidemics outbreaks induced by climatic variations.

Another point, which may cause of confusion, it is the relationship between natural selection and population dynamics. I would like to emphasize again that the models based on different Visions consider different aspects of the population, respectively, suggest a specific link evolutionary and population dynamics. As an example, Table 2 provides a comparative analysis of Adaptive Dynamics (Vision 1) and Co-selection (Vision 3) approaches. The table 2 shows that these approaches are so different that direct comparison is hardly possible, since they are dealing with a fundamentally different processes (genetic changes as result of viable mutations versus phenotypic changes as result of phenotypic plasticity) and completely different time scales (many thousands generations versus several generations). This clearly shows that the overall relationship between ecology and evolution should not be considered on two timescales (population-evolution) only, but at three (at least): population changes (within lifespan of the individual) - phenotypic changes (within lifespan of community) – genotypic changes (within lifespan of species). Note that Adaptive Dynamics approach makes a big leap between population and evolutionary timescales, totally overlooks importance of phenotypic changes.

Table 2 Basic characteristics of Adaptive dynamics and Co-selection approaches

	ADAPTIVE DYNAMICS	CO-SELECTION
Based on	Vision 1	Vision 3
Describes	Changes in genotypes	Changes in phenotypes
Underlying idea	Mutations create, environment selects	Adaptation of individuals to each other within community
Considers fitness as	Absolute property of the individual(it can be measured for each individual disregarding other individuals)	Relative property of the individual(it can be measured only by comparing individuals within community)
Make accent on such event as	Emergence of novel ecotype, which can potentially invade into resident population (viable mutations)	Changing in phenotypic structure of community through phenotypic plasticity
Considers evolutionary timescale as	Period in which viable mutation can happen	Period in which phenotypic changes can happen
Actual timescale	Thousands generations	Several generations
Main driven mechanism	Mutations	Inequality among individuals within community
Polymorphism	Can emerge as response on certain environmental condition	Always presents and plays key role in dynamics
Population dynamics changes because of	Changes in absolute trait(s), which affect net survival or reproduction can happen	Structure of community changes
Key words	Viable mutations, novel ecotype, invasion fitness,	Phenotypic plasticity, competitiveness distribution,

In the end, I would like to express my attitude to the modelling in general. For me (as a physicist by basic education), the modelling is nothing more than finding a path from one crucial experiment to another. I would like to emphasize that most results obtained in this thesis can be directly tested in experiments (feature that is not often found among the various biological theories, which tend to focus more on our understanding of nature than nature itself). In part, Paper V offers a design of such experiments with microorganisms.

Introduction

The role of individuality within the community has long been the focus of researchers. In the foreword to Adam Lomnicki's *Population ecology of individuals*, Robert May wrote:

> A common tendency in the field of population ecology has been to overlook individual differences by treating populations as homogeneous units; conversely, in behavioral ecology the tendency has been to concentrate on how individual behavior is shaped by evolutionary forces, but not on how this behavior affects population dynamics. Adam Lomnicki and others aim to remedy this one-sidedness by showing that the overall dynamical behavior of populations must ultimately be understood in terms of the behavior of individuals.

In preface of this book Adam Lomnicki wrote: "This book has been written with the conviction that further progress in ecology requires taking into account the fact that ecological systems are made up individuals that differ among themselves, and not only in their taxonomical affiliation, sex, and age…". However, in spite of overwhelming amount of empirical evidence and wide agreement among ecologists, since 1988, when this book has been published, such an approach has not become widespread. This is perhaps partly because a proper analytic model able to connect classical population dynamics with an emergent property of interacting individuals has not yet been made; partly because of the appearance of an individual based approach (IBM), new of that time, which many believed would solve the issue by extensive computer calculations (DeAngelis, D.L., Rose, K.A., and Huston, M.A., 1994.); and partly because the addressing of fundamental questions does not provide the intellectual comfort which statistical modeling of empirical data on particular species does.

Nevertheless, in the last decade it has become apparent that neither computer power nor sophisticated statistical treatment of empirical observations can ensure the smooth transition from quantity of data into quality of knowledge (Grimm V., 1999.). A new paradigm is still required for the further development of ecology, as Adam Lomnicki and others anticipated more than 20 years ago. Moreover, demand on such an integrated paradigm, which is able to fill a gap between individual and population scales and to put a species-specific physiology, collective behavior, population dynamics and natural selection into a unified analytical framework, is constantly growing (Johnson M. T.J. and Stinchcomble J. R., 2007.). Without it, the amount of specific data and excellent studies of particular species remain confined to an empirical context and an extensive biological knowledge does not transfer into a broad ecological theory.

Previous studies have tended to either ignore individual differences completely (classical population models), or simulate the life-history of each individual as absolutely unique (individual based models). The obvious benefit of the approach presented here is that it avoids both extremes; on the one hand, it acknowledges the existence of individuality, but on the other hand considers individuality itself to be a product of interactions among individuals within the community. Classical population models have such valuable theoretical assets as analyticity, but, at the same time, their ability to model the real situation is severely limited. IBM models, meanwhile, can include for consideration the smallest details of individual behavior, but are not able to produce general analytical results. The

CCDM approach aims to cut this Gordian knot and create a mathematical base for analytical models that would nevertheless include some benefits of IBM. The secondary goal of this study is to demonstrate how it works on several applications.

Brief sketch of ideas

This chapter provides an informal simple description of key terms, concepts and methods underlying the CCDM approach, as well as attempting to anticipate possible reader questions and give answers to them.

As a prologue to the general idea of this thesis, it is easiest and perhaps clearest to start by considering a very simple, almost biblical question: How to divide, for example, 1000 loaves of bread among the members of one community, so that the size of this community (in the long-term) would be maximal and stable? Assuming that (i) each individual who receives less than one loaf during this period dies of hunger, (ii) the individual can reproduce (say, for example, two offspring), if he or she gets more than three loaves, and (iii) in other cases, the individual can survive, depending on his or her age, but not reproduce. It is easy to see that if all the food is given to only one individual, the size of the community will be stable and equal to one individual. On the other hand, if the food is evenly divided between individuals, the size of the community will constantly fluctuate between 333 and 999 individuals. Moreover, if fertility had been more than two, then the community, under this type of resource allocation, would become extinct. Therefore, neither highly unequal nor equal distribution of resources answers the question. However, we can introduce a function of resource allocation in which the level of equality can change, and then find an exact value for this level, which maximizes the stable size of the community. For this puzzle, the maximum stable size is 555 individuals and it corresponds to the *level of inequality* (measured by the Gini index) equal to 0.289. Of course, this is a toy example; nevertheless, it reveals how the level of inequality in the distribution of resources can critically affect population dynamics.

It is apparent that in the real community, the level of inequality is not set by someone's will, but is itself the result of the inherent inequality between individuals and stochasticity in the processes of obtaining and allocating resources. There is a second question: What trait can sufficiently describe the differences between individuals within the community? It is clear that individuals differ in many respects, including age, sex, size, aggressiveness, a place in the social hierarchy and so on. From this, it follows that such a *functional trait*, to a certain extent, should include all these parameters, which makes it extremely difficult for the direct determination.

However, we can advance the issue by observing the other side of it, namely, by asking - What determines the reproductive success of the individual within the community? I assume the answer to this to be its *competitiveness*, i.e. its ability to provide a resource for its own survival and reproduction, which can be measured directly in units of resources or the energy content of resources. For this approach, the idea of a functional trait such as competitiveness is a key concept. It should be noted that competitiveness is a relative measure and is linked to a particular community, which can in turn be described by the *frequency distribution of competitiveness*. It could be asked whether the distribution of the competitiveness is a distribution of resources, the answer to which would be: Yes, it is, but only in the absence of stochasticity. Otherwise, this distribution must be understood as an underlying distribution of opportunities to obtain resources. Someone might also ask whether the distribution of competitiveness is stable. The answer to this would be that it obviously depends on the size of the community and the amount of available resources.

Here we come to the second key concept of this approach: although the distribution of competitiveness is not stable, its *shape*, which reflects the relative level of equality in the

community, is stable over a short (less than one generation) timescale. The reason for this lies in the fact that the structure of the community cannot change quickly in response to changes in resource availability, although such changes do occur over generations. This allows for the dividing of parameters of the competitiveness distribution on a density-independent *shape parameter* and density-dependent and resource-dependent *scale parameter*.

It is important to emphasize that the distribution of competitiveness is the outcome of various intra-community interactions in the sense that it is a description of intraspecific interaction. This mode of description is non-standard for ecological literature, which mainly focuses on the pairwise interactions between individuals or species. However, this mode of description of complex systems is common in the fields of physics and economics. In physics, a system consisting of many interacting particles is described by way of the energy distribution, while in economics market competition is described by an index reflecting the level of inequality in the distribution of firms by size. Similarly, we describe the intra-community interaction with the shape parameter that reflects the level of equality in the distribution of opportunities to obtain resources.

There arises the subsequent question as to what can change the shape of the distribution of competitiveness, and how it can do so. The answer provides another key to this approach: if competitiveness can be inherited in some way, then natural selection ensures that, in the community, the proportion of offspring of highly competitive individuals, who are themselves eligible for highly competitive positions in the community, will steadily increase. It should be noted that competitiveness is a relative value, and this selection model hence differs from classical ones on the following points: (i) The aptitude of the individual depends on its competitiveness with respect to the performance of other members of the same community; (ii) Although the proportion of offspring of highly competitive parents grows, this does not necessarily lead to an increase in the mean competitiveness, since the difference between competitiveness falls. This is not a paradox, but rather a consequence of the fact that to win in the competition an individual does not have to be the absolute best, but simply good enough to be only slightly better than other contenders. In other words, the result of competition for resources is determined not by absolute values of certain traits, but their relative differences. This is the main difference between this type of selection and adaptation to environmental conditions. In this sense, we can say that we here consider selection to be a form of adaptation of individuals to each other, subject to the constancy of the environment. In this thesis, we introduce a special term for this kind of selection, *co-selection*, which is in some ways analogous to the term co-evolution, but applies to the scale of conspecific community. You may also notice that in contrast to adaptation, co-selection does not require changes in the physiology of the species, and it can thus occur much faster. Thus, this approach considers, perhaps, the “fastest” evolutionary timescale at which physiology of the species does not change and is only a change of phenotypic structure of the conspecific community. Unfortunately, this kind of "fast" evolution has never been a major focus of evolutionary researches, but the situation is now changing, because this issue has great practical implications. The approach suggests that the co-selection process can be a main driver behind the “fast” evolution and is intended to fill the gap between the co-selection (several generations) and adaptive (a few thousand generations) time scales.

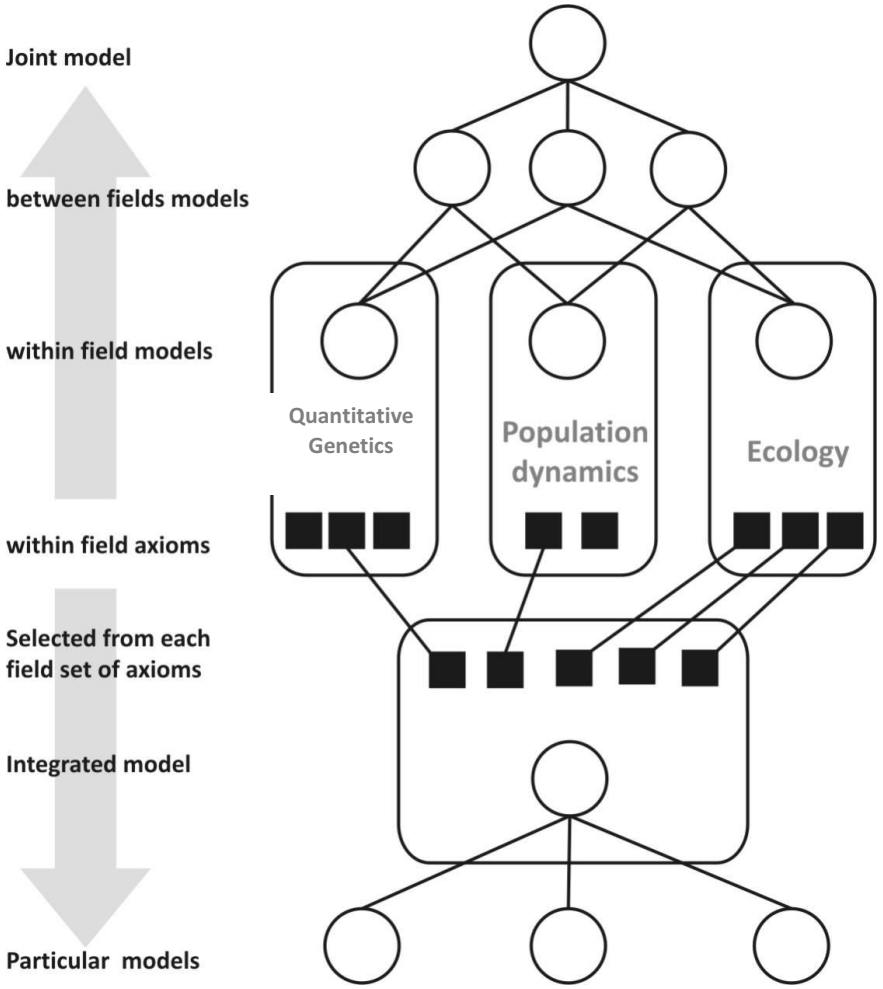


Figure 1| Two methods of synthesis of several related disciplines. There are two directions of development of interdisciplinary models: the interweaving of individual branches or the merging of the roots. This thesis pursues the second way.

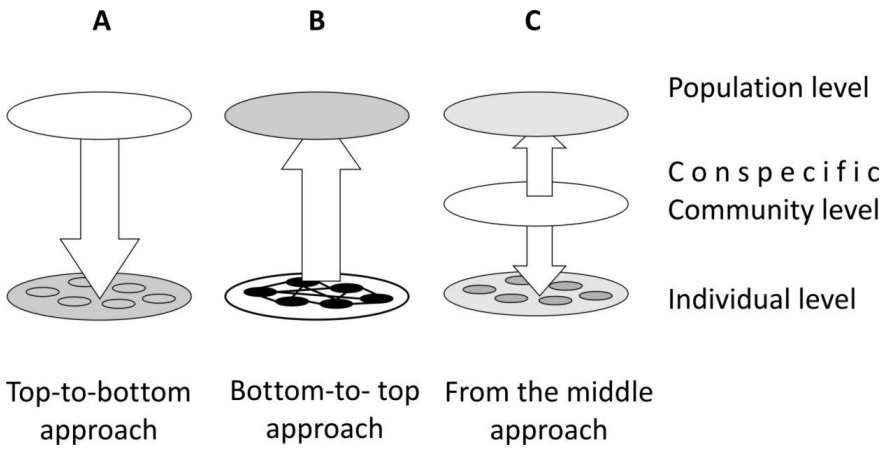


Figure2| Three ways of looking at population dynamics. (a) Top-to-bottom (Classical population models): this approach evaluates how properties of virtual "average" individual can affect the birth-death balance. In this sense, it considers all processes on the population level; (b) Bottom-to-top (Individual based models): this approach directly simulates the effect of pairwise interactions among individuals, and hence considers all processes on an individual level; (c) From the middle (Conspecific community models): this approach introduces an additional intermediate (conspecific community) level. It considers birth-death as individual level processes, while the resource allocation as community level process.

What is new about this approach? Although most of the ideas presented here are not new, it is necessary to emphasize several points that may seem unfamiliar to ecologists and biologists.

(i) The method of the synthesis of various disciplines (Figure 1) is a classic axiomatic method, widely used in the fields of physics and mathematics.

(ii) The method of modeling the population dynamics (Figure 2), which introduces an additional interim scale of the population (conspecific community scale), is the classic method of statistical physics, which makes replacement of individual interactions between objects on the distribution function of these objects with respect to energy within a certain system.

(iii) Although the idea of co-evolution is a standard for evolutionary biology, its use on the scale of conspecific community is unusual, as is the introduction of such functional traits as competitiveness.

(iv) As a way of including of stochasticity into models, here we use a method similar to that of the grand canonical ensemble, which is used in statistical physics, namely, we consider an infinite number of independent replicas of the same community, and each replica, depending on the realization of the random process, has its own dynamics.

Paper I. Conspecific Community Dynamics

How are population dynamics and natural selection connected? In this article, we try to answer this general question by way of the CCDM approach. We consider a certain timescale and population-specific scale, that it, we consider the process of co-selection within the closed conspecific community. Much of this article can be viewed as a formal introduction to the CCDM approach. Particular emphasis is placed on the comparison of this approach and other approaches to modeling the interdependence of population dynamics and natural selection. On the basis of several particular examples, the paper shows that, depending on the initial level of equality, co-selection may lead to a decrease in the number of members in the conspecific community. We discuss the possibility of applying this approach for modeling the process of rapid evolution. The paper also introduces a general framework for further applications.

Paper II. Rethinking the basis of the population growth

What limits population growth? Since Malthus, this has been probably the most fundamental question of population dynamics. After more than 200 years of investigation, it is rather difficult to expect any radically new responses to it, but the CCDM approach nevertheless offers a fresh perspective on this topic. Perhaps the key point of this approach is that we include in consideration the fact that an individual lives in the conspesific community, where its survival and reproduction depends on other members of the same community. Thus, community structure, expressed as the level of inequality of competitiveness among members, may be a major factor influencing population growth. Another point that we take into account is that the ability of the community to provide resources for itself depends on the number of members and of their performance. We show that if the performance of an individual (the number of resources that it adds to the virtual resource pool) decreases along with the increasing strength of the community, population size remains limited in spite of an unlimited number of available resources. However, the most intriguing results are obtained if one considers the fact that community structure can evolve under the influence of co-selection. In this case, the overall average demographic characteristics of the community and the relevant life-history traits undergo certain changes. Consideration of these circumstances leads to some far from trivial conclusions:

(1) The so-called economic-demographic paradox (the inverse relationship between average fertility and the average per capita amount of resources) is not a paradox, in the sense that it does not violate any of Malthus's assumptions. Instead, such behavior of the average birth rate is a direct consequence of changes in the level of equality in the community under the influence of co-selection. In other words, fertility is reduced simply because of a lack of resources. It could be asked how this can happen, if the average number of resources per individual grows. The answer is contained in the word *average*; the growth of *average per individual* amount of resources does not mean that *each individual* within the community receives a surplus amount of resource required for reproduction. It might also be asked on what these additional resources are spent. These resources are redistributed in the community so that more individuals receive sufficient resources for survival (which leads to an increase in average life expectancy); at the same time, however, fewer individuals receive sufficient resources for reproduction (which leads to falling birth rates). This example shows how important it is to take into account the inequality among individuals in population-based studies, as otherwise a pseudo-paradox such as this

one may occur. This result is important also because several decades have been spent on the search for evolutionary explanations for the demographic transition phenomenon. Unfortunately, this quest originally started from such a paradox. Correspondingly, answers being sought among the various behavioral mechanisms are far from the basic tenets of Malthus. This study shows that the demographic transition can have a simple biological explanation that does not require additional behavioral hypotheses.

(2) Population growth may be limited by natural selection. This is quite an unusual result, as it is traditionally believed that natural selection leads to an increase in fertility, which in turn accelerates population growth, which can be limited by lack of resources. However, taking co-selection into account changes the perspective. The fact is that in a closed conspecific community, natural selection leads not only to the "survival of the fittest", but also to equalization of competitiveness among individuals. In turn, this increases the level of equality in the community, which can reverse population growth from positive to negative.

(3) Under certain conditions the conspecific community may not have the carrying capacity (birth rate not equal to death rate) that is to be unbalanced during the period of its existence. The dynamics of such conspecific community can be described as the succession of characteristic phases of development, within which the dynamics of birth and mortality rates are in a certain ratio. It is interesting that the description of these phases and the process of change are very similar to empirical models of demographic transitions. We suppose that the CCDM approach can provide an analytical platform for modeling of such unbalanced demographic processes.

Paper III. Shoal-based approach to the fish population dynamics

Why are fish so involved in collective behavior? How does this behavior affect the population dynamics? In this paper, we propose answers to these questions within the CCDM approach and an optimal shoaling model (OSM). In OSM, we consider the effect of hydrodynamic efficiency, which arises from the collective motion of fish. We show that a tradeoff between amount of food intake and the expenditure of energy on locomotion leads to three characteristic spatial configurations of shoals, which are optimal for certain types of activity. Then we show how the size of the shoal can influence the effective energy consumption. In turn, the CCDM model helps to relate this consumption to the dynamics of populations. The model shows how involvement in collective behavior, species physiology and hydrodynamic characteristics of the fish species are associated with bi-stability and density-dependence. Of particular interest is that, under certain parameters, this model gives a good approximation of the standard empirical models of fish populations. In this sense, we can consider this model as a derivation of empirical models from first principles.

This model may be useful in resolving the long-term confusion about density-dependence, or the so-called recruitment problem. Firstly, the model clearly shows that the density-dependence is a threshold phenomenon. Secondly, the density-dependence is one-sided (asymmetrical) phenomenon. Thirdly, the degree of expression of these thresholds strongly depends on the level of equality in the shoal. Finally, these thresholds are not constant but change with the changes of availability of shoal resources, i.e. thresholds are resource-dependent.

Analysis of the model shows that the bi-stability can occur in populations in two dissimilar cases. First, in the case of very strong effect of hydrodynamic efficiency, this may arise for species with larger body size and high speed. Secondly,

in the case of strong cannibalism, this may occur for the species forming a multi-cohort shoals.

The shoal-based approach to fish population offers an integrated analytic platform for interdisciplinary studies. We emphasize that further development of the fisheries ecology and fish population dynamics cannot be confined only to the improvement of techniques of statistical analysis of time series, but requires co-development of analytical models that are able explicitly to take into account the physiology of fish species, their collective behavior and resources. We can presuppose that it may find application in several areas: (i) statistical analysis of empirical data (time series), (ii) a shoal-based management, and (iii) comparative evolutionary studies.

Finally, our study highlights the importance of looking at species shoaling behavior and physiology when analyzing the population dynamics. We have shown how these aspects can affect the density-dependence and bi-stability. In management of fish stock, it is important to have an understanding of these processes. Collectively, the shoal-based approach should improve our analytic understanding of fish populations and may enhance our tools for forecast.

Paper IV. Epidemiology of conspecific community

How does the inequality among individuals affect the spreading of infections? How can the resource variation affect the outbreak of epidemics? What do we need to know in order to improve the reliability of epidemic forecasts? These are issues of great practical interest, and the answers to which are offered by CCDM approach.

The paper introduces an integrated approach to modeling epidemics that combines nutrition-dependent physiology and nutrition-dependent immunology of an individual with differences among individuals within a conspecific community. We assume that individual susceptibility, resilience, infectiousness and loss of immunity depend on individual resource intake. Thus, the approach allows for the reconsideration of the classical epidemics models in respect of two essential points: heterogeneity among individuals and the underlying physiology of host.

In this paper, we consider only one particular example of the use of the CCDM approach in field of epidemiology. Nevertheless, even this simple example demonstrates the important implications that an inclusion of heterogeneity among individuals in a host community can have. We demonstrate that traditional characteristics used to predict the epidemic, such as the population size or the average physical condition of the host, could not work properly in cases of heterogeneity.

The model shows that depending on the time scale and the level of equality in the host community, the resource variation can have completely a different effect on the probability of epidemics. A sharp drop in resources increases the probability of epidemics in communities consisting of relatively equal individuals, but in communities consisting of unequal individuals, this leads to a decrease in the probability of epidemics.

We have emphasized that an understanding of epidemic processes in heterogeneous communities requires a paradigm shift from the focus on population size and overall physical condition of the host to focus on the level of equality in the community and underlying species physiology (including immune system). Of course, it was widely recognized that the heterogeneity should be somehow included in the model of epidemics, but analysis reveals, surprisingly, that the role of heterogeneity can be so significant as to fundamentally alter the main results of the classical

epidemiological models. For example, the SIS model, which in the classical variant can either not have the epidemic threshold (in the case of standard incidence) or have only one threshold value (in case of mass action incidence), with the inclusion of heterogeneity may have a pair of thresholds in both cases.

Finally, the approach opens a new way for interdisciplinary integrated research, which allows for the incorporating of the physiological and immunological studies of an individual with ecological studies of conspecific communities. These researches may provide not only theoretical interest, such as the clarification of fundamental mechanisms behind the host-pathogen interaction under evolutionary and environmental changes, but more importantly, may be purely practical. For example, they can significantly improve the accuracy of epidemic forecasting by taking into account heterogeneity of immunocompetence among individuals. In view of that, vaccines against many infectious diseases give only a partial effect that depends on the condition of the individual; such studies can help to design a vaccination program more accurately.

Paper V. Modeling the interactions between conspecific communities

How can the self-organization of individuals within the conspecific community influence the interaction between communities? In this paper, we begin the discussion of this issue and consider several models of interaction between communities. Perhaps the main difference between these models and the classical models of ecological interactions is the presence of conspecific community scale, which adds additional dimensions to the consideration. In other words, we consider the interaction between individuals and the interaction between communities separately. Another feature of these models is that they always take into account the resources in an explicit form, which gives an opportunity to revise the classical model in this aspect.

This paper does not aim to obtain general results, but rather to demonstrate in several examples how the conspecific community model approach tackles basic ecological interactions in comparison to the classical models. The paper develops CCDM models for the predator-prey system, competition for resources and such interactions, nonstandard for ecological theory, as warfare.

This approach provides a new interpretation of the results for the model of competition for resources and establishes an additional classification of such models, which take into account the effect of cooperation and adverse effects. In addition, models offer a possible explanation of the paradox of the plankton. The explicit solution of the pure resource competition model gives an interesting relationship between the total number of all organisms, species diversity (variation in the “carrying capacity” between species) and species richness (number of coexisting species).

Finally, we introduce a model for specific interactions between conspecific communities, which can be called “warfare” and which represents a mixture of resource competition and mutual extermination. Among other things, the model offers a mechanism explaining the occurrence of toxic algae blooms. The principal feature of this mechanism is that it considers the toxicity not as defense against predators, but as a special form of resource competition between different phytoplankton species. In other words, this approach explains the toxic bloom as the continuation of resource competition by other means, including "chemical warfare" by the toxin.

Perspectives

Further development of this work is seen in two promising directions, theoretical and practical. Theoretical development involves the further expansion of the model by taking into account co-selection in terms of migration between communities, as well as the inclusion of mutations. Preliminary estimates show that migration can be a vital influence on the outcome of the selection process. For example, it makes possible the existence of multiple selection-stable states. It may be suggested that it is the existence of these states that may be the initial phase of reproductive isolation. Further, the inclusion of the mutation will allow the tracing of the process as two conspecific communities located in different selection-stable states can evolve into two different species. The novelty of this approach is that it allows for the taking into account not only of the adaptation to the abiotic environment but also the adaptation of individuals to each other (biotic environment). This will help to clarify the answer to one of the major issues of evolutionary theory: What factors (biotic or abiotic) are the key to evolution?

In the context of applications, this approach can be used, right now, in areas that connected in one way or another with population dynamics and where the existence of the individual in their collective nature cannot be neglected. In fact, it suggests an upgrade from classical analytical framework (which is based on classical population models) to the analytical framework, which the CCDM approach offers. In this thesis, there are several examples of such use. It should be noted that this is just the beginning, which nevertheless already provides enough interesting results. I would especially like to note that this approach allows one to specify various interdisciplinary questions, such as: How does cannibalism affect the outbreak of epidemics? How does the demographic transition relate to the spread of infectious diseases? How can co-selection influence the outcome of war? Production of such questions by themselves is not unusual, but this approach makes these questions mathematically well-defined and respectively allows an analytic solution.

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Paper I

Conspecific community dynamics

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Abstract

There is general agreement that further development of ecological and evolutionary studies requires a new interdisciplinary analytic platform tha can link short-tem population dynamics processes with long-term evolutionary processes. We argue that the performance of this enormous task could begin to focus on specific population level and timescale. We suggest that such a beginning reference point could be a co-selection operating at the level of conspecific community. We think that the fact that single-species organisms within a population organize themselves into communities has deep natural reasons and cannot be simply ignored; furthermore, this fact may become a key point of the synthesis of ecology and evolution. Here, we introduce an analytic approach, which considers conspecific community dynamics as interdependent processes of population dynamics and natural selection.

1. Introduction

Historically, the issue of connection between natural selection and population dynamics was approached from three different perspectives: population ecology, population genetics and evolutionary biology. In the last decades, there has been a trend toward the increasing integration of these perspectives [1]. Nevertheless, it became clear that the integration of such dissimilar approaches can hardly be implemented at the level of mechanical combination of existing models, and requires the return to the level of basic principles. At least two conjunctions require significant changes: (i) a population model is required that explicitly takes into account the difference between the fitness of individuals, and (ii) a selection model is required that explicitly takes into account the mutual interdependence between fitness of interacting within the conspecific community individuals. Therefore, a functional trait [2] that, on the one hand, would be decisive for fitness, and on the other hand, would reflect the relative nature of fitness within the community, is required. We consider competitiveness of the individual to be such a trait (see glossary). Thus, on one hand, an ability of the individual to provide itself with food determines its reproductive success, and, on the other hand, the competitiveness of the individual clearly depends on the performance of the other members of the same community. We also consider that a distribution of competitiveness is not some arbitrary volatile value, but rather a reflection of such relatively stable aspects of the conspesific community as the demographic structure, organizational hierarchy and the type of intra-community competition. Regarding the last aspect it should be noted that, traditionally in the field of ecology, intraspecific competition is seen as a *process* of interaction between individuals, but in this approach, intraspecific competition is considered a certain *situation* prevailing in the results of these interactions. Such a view, in principle, is not new; indeed, it is the standard method of describing the competition in the economy, where the distribution of firms by size determines the prevailing competitive situation on the market, such as monopoly, oligopoly, monopolistic competition, perfect competition and so on.

Glossary

Conspecific community: is a self-organized stable group of interacting organisms of the same species, which somehow acquire and share resources. Distinction from close term (local) population lies in the fact that the community has a certain behavioral and organizational boundaries that allow for the distinguishing of members of one community from another. One conspecific community always represents some (local) population, but the converse is not always true: the (local) population may consist of several communities. In general, the term conspecific community is used here as a replacement for the many species-specific terms such as pack, flock, family, colony, herd, swarm, shoal and so on.

Competitiveness: is a comparative measure of the ability of a member of a conspecific community to acquire some share of the available (for a given community) resources. Competitiveness is measured as the *a priori* expected amount of the resources that may be obtained by a member of the community through interactions with the environment and other members of this community. Presumably, such competitiveness is a function of all traits that can affect the success in obtaining the resource. In turn, individual fitness is a function of competitiveness.

Competitiveness distribution: is a frequency distribution of individuals with certain competitiveness within the same conspecific community. In the absence of stochasticity, this distribution is exactly equal to the distribution of resources among members of the community; otherwise, it is a prior distribution of opportunities to obtain a certain amount of the resource. Distribution of competitiveness may be characterized by the shape and scale parameters.

Shape parameter of competitiveness distribution: a density and resource independent measure that quantifies the relative level of equality of opportunities to obtain resources among members of the community.

Scale parameter of competitiveness distribution: a density and resource dependent measure that quantifies the scale of a particular community.

Physiological (response) functions: are a relationship between the competitiveness, the quantity of consumed resources and life-history events of the individual. Basic physiological functions describe competitiveness: nutrition-dependent survival and reproduction or, in the simple case, nutrition-dependent survival and reproduction of the individual. Other physiological functions may describe, for instance, nutrition-dependent susceptibility, infectiousness, recovery, loss of immunity and so on.

Co-selection: is a natural selection process in which the reproductive success of the individual depends on its competitiveness, which in turn depends on the competiveness of other member of the same conspecific community.

Conspecific Community Dynamics Model (CCDM): is a system of difference or differential equations, which describe the short-term population dynamics of the community in mutual connection with the long-term (driven by concurrent natural selection) dynamics of the competitiveness distribution. Short-term population dynamics related to the time scale approximately equal the lifetime of the organism without consumption of any food. Long-term dynamics associated with a time scale equal several generations.

Similarly, the shape of the distribution of competitiveness can describe the level of equality between members of the conspecific community, as well as determining the type of intra-community competition. Thereafter, if we assume that competitiveness can be somehow inherited, then the distribution of competitiveness is slowly changing with the change of generations, because individuals that are more competitive will leave more offspring, which in turn (in absence of migration) will qualify for the same competitive position as their parents. Thus, through the distribution of competitiveness, short-term population dynamics may be associated with the long-term effect of natural selection.

2. Theoretical framework

The General Conspecific Community Dynamics Model (CCDM) should include the following basic components: inequality between individuals within the community, stochasticity in the resource allocation, species physiology and natural selection. In addition, it should reflect such aspects of the community as foraging behavior, the dependence of available resources on the community size, the stress effects of overcrowding, general demographic and the life-history of the individual. Within the Individual Based Model (IBM), the approach [3-7] to constructing such a computer-simulated model is not difficult. However, it should be noted that we aim at a very different goal, namely, obtaining an analytical model, i.e. a model that explicitly examines the causal relationships.

It is convenient to present the derivation of the CCDM model in the manner of the axiomatic approach, which allows for the separating of the initial assumptions (axioms) from the subsequent conclusions. This framework ensures that any conclusions, no matter how unusual they may seem at first glance, can be traced back to these basic assumptions (Box1). These axioms are chosen from different areas of ecology, population genetics and evolutionary biology, and represent indisputable postulates in these fields. Some of these axioms seem to be obvious, respectively, and are not necessary, but it is not. For example, the axiom of the existence of individuals is not used in classical population dynamics, and models based on it could as appropriately be applied to the population as to the biomass. Such a universal “top-to-bottom” approach, which requires minimal knowledge about a population, can be extremely useful for statistical estimates of population size, but hardly suitable for evolutionary studies, because it simply neglects the existence of individuals. In turn, a “bottom-to-top” approach (like, IBM or multi-agent models), which, in principle, can proceed from the basis of any facts about the behavior of the individual, do not take into account the collective nature of individuals, their tendency to gather in a self-organized community. The main feature of this approach is that it not only strictly separates the processes that going on the “top” (population) and “bottom” (individual) levels, but also introduces another “intermediate” level, which represents the conspecific community. Furthermore, in contrast to the classical population models, where the birth-death processes are considered at the population level, and unlike the IBM model, where all processes are considered at an individual level, CCDM models view the process of birth-death at the level of the individual, but the distribution of resources and intraspecific competition at the community level. In other words, this approach emphasizes that the process of obtaining and allocating resources is collective in nature, in which individual success is highly dependent on the performance of other members of the same community. Again, we emphasize that this is not a new idea. In fact, it is one of the key propositions of community ecology. However, here we apply it to another level, namely, we assume that the self-organized group of organisms of one species also represents a community – the conspecific community.

Box 1. Axioms behind the CCDM approach

The CCDM approach is based on the next set of basic axioms:

I. **First basic Malthusian proposition**: Any organism can appear only as a result of birth by a parent organism.

II. **Second basic Malthusian proposition:** Survival and reproduction of each organism requires a certain amount of consumption of resources. (These amounts are determined by the physiology of the species.)

III. **The existence of individuality:** A conspecific community can consist of individuals that are unequal by their competitiveness.

IV. **The existence of intrinsic organization:** Various interactions within the conspecific community can lead to the establishment of the relatively stable shape of the competitiveness distribution.

V. **The existence of co-selection:** Reproductive success (fitness) of the individual within a conspecific community depends on their competitiveness and, consequently, on the performance of other members of the same community.

VI. **The existence of inheritance:** In a closed community, the offspring of highly competitive parents have a better chance of taking a highly competitive position in the community than the descendants of the less competitive parents.

The first two axioms are basic for the population dynamics; the last two axioms define the process of natural selection, while the middle pair of axioms acts as a link between. This set of axioms provides a convenient basis for comparing different approaches.

Classical population models are essentially based on the first axiom. To some extent, the second axiom is also used as the origin for the concept of a carrying capacity, but it should be noted that the carrying capacity is a property of the whole population, and is not linked directly with any properties of the individual organism, as the second axiom originally claim.

IBM models can be based on any of the axioms, except the fourth, because they simulate the effect of pair interactions between individuals and do not *a priori* assume the existence of any organization. In contrast, the CCDM approach assumes that a wide variety of interactions (not necessarily pairwise) eventually leads to a certain distribution of the competitiveness. The difference is that the IBM approach sees resource competition as an individual level process, while the CCDM approach is seen as a community level outcome of this process.

Classical population genetics assumes that, for any given environment, fitnesses are independent of population density and of the frequencies of other genotypes, and is therefore based on the axiom of inheritance alone. To some extent, the fifth axiom is used as the starting point for the concept of a frequency-dependent selection. However, it should be noted that the frequency-dependence supposes some implicit connection between fitnesses, while the fifth axiom supposes explicit dependence between individual competitiveness within the conspecific community.

It should be noted that CCDM models include stochasticity, using a method similar to that of the grand canonical ensemble [8], which is used in statistical physics. That is, we consider an infinite number of independent replicas of the same community, and each replica, depending on the realization of the random process, has its own dynamics. The number of community that appears in the models is always the result of the averaging of the replicas.

This is unlike those of classic models of population models with stochasticity, which consider a single replica and spend an average over time.

Table1. Interpretation of notations

Notation	Interpretation
N	Number of the individuals in the conspecific community
R	Total amount of resources available for given community
s	Competitiveness of the individual
ε	Amount of consumed by the individual resources
$b(\varepsilon,s)$	Physiological (fecundity) response function
$d(\varepsilon,s)$	Physiological (mortality) response function
k	Shape parameter of competitiveness distribution
$\theta(N,R)$	Scale parameter of competitiveness distribution
$S(s\mid k,\theta)$	Competitiveness distribution
$P(\varepsilon\mid s)$	Stochasticity distribution
$E(\varepsilon\mid k,\theta)$	Resource distribution
$\overline{W}(N,k)$	Crude average birth rate
$\overline{D}(N,k)$	Crude average death rate
$W(s)$	Expected numbers of offspring (absolute fitness) of the individual
$D(s)$	Expected mortality of the individual
$w(s)$	Relative fitness of the individual
h	Heredity coefficient
$I_z(x,y)$	Regularized incomplete beta function

Population equation

The population dynamics of a conspecific community can be described in the same manner as is done in classical population models, namely, as a balance equation for the birth-death process (Table 1)

$$\dot{N} = (\overline{W}(N,k) - \overline{D}(N,k))N \quad , \qquad (1)$$

which is taken under the condition of constancy of the shape parameter of competitiveness distribution. Then, the crude average birth and crude average death rates can be subjected to decomposition and are presented as the following integrals

$$\overline{W}(N,k) = \int_0^\infty W(s)S(s\mid k,\theta)ds$$
$$\overline{D}(N,k) = \int_0^\infty D(s)S(s\mid k,\theta)ds \qquad (2)$$

In practice, we here simply replace the word "average" with its mathematical formulation. In the next step, we continue the decomposition and replace the expected numbers of offspring and expected mortality rates on the following integrals

$$W(s) = \int_0^\infty b(\varepsilon, s) P(\varepsilon \mid s) d\varepsilon$$
$$D(s) = \int_0^\infty d(\varepsilon, s) P(\varepsilon \mid s) d\varepsilon \qquad (3)$$

which, in essence, is a replacement of the word "expected" by its mathematical expression. As a result, we obtain the complete expressions for $\overline{W}(N,k)$ and $\overline{D}(N,k)$ that use only the basic components

$$\overline{W}(N,k) = \int_0^\infty \int_0^\infty b(\varepsilon, s) P(\varepsilon \mid s) S(s \mid k, \theta) ds d\varepsilon$$
$$\overline{D}(N,k) = \int_0^\infty \int_0^\infty d(\varepsilon, s) P(\varepsilon \mid s) S(s \mid k, \theta) ds d\varepsilon \qquad (4)$$

In turn, the resource distribution can be calculated as a posterior distribution of a prior competitiveness distribution:

$$E(\varepsilon \mid k, \theta) = \int_0^\infty P(\varepsilon \mid s) S(s \mid k, \theta) ds \qquad (5)$$

Here we take into account the fact that the expected amount of resource, which is a measure of competitiveness, may differ from actual consumption of resources, or, more simply, we consider the randomness in the process of obtaining resources. We can then calculate the mean value of both competitiveness and resource distribution:

$$\bar{\varepsilon} = \int_0^\infty \varepsilon E(\varepsilon \mid k, \theta) d\varepsilon$$
$$\bar{s} = \int_0^\infty s S(\varepsilon \mid k, \theta) ds \qquad (6)$$

Assuming unbiased expectations $\bar{s} \equiv \bar{\varepsilon} = R/N$, we can obtain (for given types of $P(\varepsilon \mid s)$ and $S(s \mid k, \theta)$) an explicit expression for the scale parameter $\theta(k, R, N)$. This expression completes the formulation of equation of population dynamics for a conspecific community, i.e. we have the necessary conditions for solving the balance equation (1) for a given value of "free" parameter k , which represents the level of equality among the individual within community. Then we proceed to the second part of CCDM model, which describes how this level of equality is changing under the influence of natural selection.

Selection equation

In a closed (without emigration and immigration) conspecific community consisting of unequal members, where individual fitness depends on the competitiveness of the individual, selection pressure leads to a change in the distribution of competitiveness in the direction of increasing the relative share of more competitive individuals. In the first approximation, we can neglect the detailed description of the process of increasing the competitiveness of the individual throughout his lifespan, because we assume the time scale is much larger than the life expectancy of the individual. Under these conditions, we can describe the selection in the form of quasi-replicator equation

$$\frac{d}{dt} S(s \mid k, \theta) = hS(s)(W(s) - \overline{W}(N,k)) \quad , \qquad (7)$$

which differs from the standard replicator equation only in the presence of heredity coefficient that means that the individual does not fully inherit the parents' competitiveness,

but has a better chance of building its competitiveness up to their level. Left side of the equation (8) can be rewritten as

$$\left(\frac{\partial S(k,\theta)}{\partial k}+\frac{\partial S(k,\theta)}{\partial \theta}\frac{\partial \theta}{\partial k}\right)\dot{k}\equiv a(s,k)\dot{k} \qquad (8)$$

Then, after averaging both sides of the quasi-replicator equation (8) for s we can get

$$\dot{k}=h\overline{A}(k)\overline{W}(k)(\overline{w}(k)-\overline{s}(k)) \quad , \qquad (9)$$

where $\overline{A}(k)=1/\int_0^\infty sa(s,k)S(s)ds$, $\overline{s}(k)=R/N(k)$, and $\overline{w}(k)=\frac{1}{\overline{W}(k)}\int_0^\infty sW(s)S(s)ds$ is a mean relative fitness. Thus, equation (9) gives a description of the process of changing the level of equality in the conspecific community under natural selection, and with the population equation (1), in principle, can give a general solution for CCDM models. However, it should be noted that obtaining an accurate general solution of this system is difficult. Nevertheless, for various special cases, you may receive as exact solutions (Box 2.) or approximate solutions with good accuracy. In some cases, general qualitative assessment of the behaviour of the path of natural selection (direction, presence and number of fixed points) may be sufficient to answer the research questions. We emphasize that, in contrast to other more general theoretical models of natural selection, this model always explicitly takes into account the physiological constrains that make it attractive to work with data.

3. Application framework

The construction of the CCDM model for particular application begins by defining three basic blocks that describe the species physiology, collective behaviour, and stochasticity in resource acquisition. (a) Species physiology is given in the form of individual physiological functions, which connect competitiveness of the individual, the amount of their consumption of resources, with its mortality and fertility. For example, in the simplest case, the physiological function can be specified as thresholds of resource consumption below which an individual dies of starvation, and above which it is able to reproduce, with the values between these thresholds signifying survival without reproduction.
(b) Collective behaviour is given by the type of distribution of competitiveness; it can be any distribution from the shape-scale family. This choice stems from the fact that it allows for the separating of the organizational structure of the community of its size, as well as connecting the shape parameter with such well-known measures of inequality as the Gini index or coefficient of variation. For example, for Gamma function, Gini index and coefficient of variation are equal to $Gini(k)=1-2I_{1/2}(k+1,k), CV(k)=1/\sqrt{k}$.
(c) Stochasticity in resource acquisition is given by the function of conditional probability, which shows what the chances of an individual with a certain level of competitiveness getting a certain amount of resource are. In other words, this function determines the degree of uncertainty to which the individual is exposed depending on its position in the community.

Further, from these basic blocks we can obtain the two intermediate blocks, which describe the distribution of resources in the community and the expected number of offspring (absolute fitness) of the individual.

Box 2. Using CCDM approach to investigate conspecific community

This example illustrates how taking inequality among individuals, stochasticity of resource distribution, physiology of the individual and natural selection into account can lead to an understanding of processes within a conspecific community. In this example, for the sake of simplicity, we assume the following: (i) distribution of the competitiveness has the form of Gamma distribution. (ii) Stochasticity of resource distribution has the form of Poisson distribution. (iii) Physiological response functions are nutrition-dependent and have a "caricature" one-step shape, which means that the individual can survive only if it acquired more than ε_m amount of resources, the individual can reproduce only if it acquired more than ε_b ($\varepsilon_b > \varepsilon_m$) resources and the individual has aging mortality rate δ and constant fecundity rate b. (iv) Total amount of resources available for the community is constant and density-independent. These assumptions allow for the derivation of simple forms for equations (1) and (9)

$$\dot{N} = \left(bI_{1/2}\left(\frac{k\varepsilon_b N}{R} + 1, k \right) + (1-\delta) I_{1/2}\left(\frac{k\varepsilon_m N}{R} + 1, k \right) - 1 \right) N$$

$$\dot{k} = ahk^{-\gamma},$$

where $a > 0, \gamma > 0$ are some parameters used for approximation of equation (10). This explicit form of the CCDM model, which is convenient for analysis, reveals several curious insights:

i. In a closed conspecific community, natural selection leads to an increase of the level of equality among individuals, and simultaneously to a decrease of the speed of this process.

ii. Under natural selection, the mean competitiveness trait declines in communities with a high level of inequality. In contrast, in communities with a high level of equality, the mean competitiveness trait growths (figure 1c).

iii. Natural selection leads to a constant decrease of the crude average birth and death rates. Eventually, the community achieves a state where the death rate becomes close to aging mortality. Starting from some level of equality, a conspecific community demonstrates the so-called "demographic-economic paradox" or inverse relationship between the average per individual amount of resource and the birth rate (figure 1d).

iv. A conspecific community has an optimal level of equality, which maximizes the population size (figure 1a). This optimal level strongly depends on fecundity rate; species with high fecundity have lower optimal levels of equality.

v. Conspesific community at a high level of equality demonstrates a lack of density-dependence on a wide range of densities $[R/\varepsilon_b, R/\varepsilon_m]$ (figure 1b). This is because the difference in amount of resources needed for survival and reproduction leads to the fact that population sizes, which maximize the reproduction and survival, also differ.

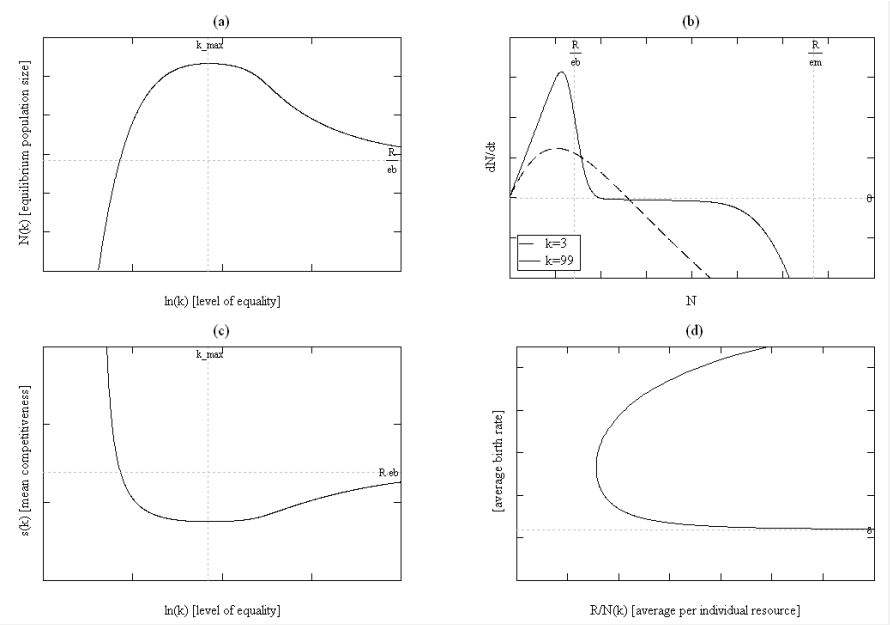

Figure 1 | Some features of conspecific community dynamics: (a) Equilibrium population size versus level of equality among individual within community. (b) Density-dependence in case of high level of inequality (dashed line) and in case of high level of equality (solid line). (c) Mean competitiveness trait versus level of equality. (d) "Demographic-economic paradox", once under the action of natural selection, the level of equality exceeds the optimum level, the birth rate continues to decline despite the fact that the average per individual resource increases.

(bc) Combining the distribution of competitiveness, which is the distribution of opportunities to obtain resources (b) and stochasticity (c), we obtain the distribution of resources. It should be noted that this block allows for the modelling a various aspects of foraging behaviour in small detail, such as the typical size of food items, the number of trials required for saturation, individual or collective nature of the foraging, density-dependence of the probability of saturation and so on. (ab) Combining the physiological function of reproduction (a) and stochasticity (b), we can obtain an explicit expression for the absolute fitness as a function of competitiveness. In next step, combining the intermediate blocks (ab) and (bc), we obtain the explicit form of the balance equation of population dynamics (1). Finally, combining it with a block (ab) we obtain the equation for natural selection (9). Some applications require a more detailed description of the community, such as, for example, one that reflects the fact that the total resources available for the community depends on population size or the fact that individuals may experience physiological stress from overcrowding. These aspects can be incorporated into the model by adding a density-dependence in the resources or physiological functions. Other applications may require the introduction of additional physiological functions. For example, for epidemic models, functions describing immunity and infectiousness of the individual may be introduced [9]. Such a detailed description of the processes within the community makes it possible to analyze the interaction between communities in all their complexity, for example, to model such multi-level relationships as warfare, as a mixture of the capture of resources and mutual extermination of rivals in a high-stress environment [11].

4. Conclusions and perspectives

What is interesting about the approach that it does not introduce any radically new ideas; instead, it is based on a set of well-known, widely accepted basic propositions (axioms). However, a careful separation of the processes occurring at the individual level with processes at the population level, as well as the separation of timescales and their subsequent reintegration at the conspecific community level gives surprisingly fresh results. Thus, despite the fact that this approach would seem not to establish any fundamentally new assumptions, it nevertheless offers a new integrated paradigm for population dynamics studies, which equally recognizes an existence of the individual and their collective behavior, the importance of species-specific physiology and the plasticity of the individual live-history, a role of natural selection and co-selection. Due to its analytical nature, the CCDM approach can be applied in any research fields that are more or less connected with the dynamics of populations, especially where the distinction between individuals and/or natural selection affects the results in some essential way. This approach has already been applied to research in demography to model the demographic transition [10], in epidemiology to model the spread of infections in a heterogeneous population and the impact of resource fluctuations on epidemic outbreaks [9], and in ecology for modeling different types of interaction between communities [11]. The encouraging results obtained in these applications suggest that the CCDM approach will become a useful tool as an analytical platform for theoretical and applied researches.

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II

Rethinking the basis of the population growth

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Abstract

The paper goes back to the basis of population dynamics, especially the works of Malthus, and tries to model his pioneering vision again, this time taking into account such of his postulates as the necessity of food for survival, the reproduction of each individual and inequities of resource distribution. We construct a Conspecific Community Dynamics Model (CCDM), which is based on these well-known postulates of Malthus. Nevertheless, analysis of the model reveals quite interesting results. (1) The size of the community nontrivially depends on the level of equality between its members (for example, there is a given level of equality in which the size of the community becomes a maximum). (2) The size of the community is limited not only by the amount of resources, but the community's ability to utilize these resources. (3) A high level of equality leads to a dynamical instability, which, in turn, under certain conditions, may lead to extinction. Thereafter, we included in the model the fact that the level of equality in the community may be constantly changing under the influence of co-selection. This in turn leads to changes in average demographic characteristics and associated life-history traits. It is interesting that this model demonstrates a so-called demographic-economic paradox, which is traditionally considered to be the main empirical argument against the Malthus theory. In conclusion, we consider the anti-Malthus or pro-Condorcet model in which resources available to the community can grow at the same pace as the population. Despite the fact that such a community has always been unstable (has no equilibrium size or carrying capacity), it may nevertheless be limited and exist for a long time due to co-selection. Analysis of this model demonstrates a significant similarity in the results with the empirical model of demographic transition.

Key words: *Malthus's Law of population growth, Malthusian catastrophe, organizational change, replicator equation, demographic-economic paradox, demographic transition*

1. Introduction

Since the release of the famous Malthus treatise, *An Essay on the Principle of Population*, scientists from different disciplines have been interested in the issue of population growth under various restrictions. In the field of population ecology, Malthus's law of population growth seemingly becomes the first principle of population dynamics (Turchin 2001). However, this law alone does not represent the main body of Malthus's work, in which he emphasized importance of such basic propositions as the necessity of food for survival and the reproduction of each individual as well as the inevitable inequity of resource distribution. These key propositions were nevertheless not included in the foundation of population

dynamics, which focuses on modeling the overall effect of population densities on population growth. Because of such a "top-to-bottom" approach, classical population dynamics is so general that it does not even require the existence of individuals as an essential axiom, and can equally be applied to biomass. On the one hand, such a view of the population as a shapeless "gray biological matter" that may increase or decrease in accordance with its own "weight" seems to be very useful for statistical estimation of population size, since it does not require any specific knowledge about the population. On the other hand, ignoring the discrete nature of organisms is a major drawback in the case of evolutionary studies, which essentially deals with the processes at the individual level. While it may be claimed that contemporary population dynamics model usually split the population into categories such as age, body size, structural classes, etc., nevertheless, within each such structural class, they still have to deal with the same repacked "gray matter".

In recent decades, several "bottom-to-top" approaches (IBM, multi-agent models, game theory modes) have tried to fill the gap between individual and population levels. However, such a narrow focus on the individual level, seemingly, has own difficulties. They either involve only one simple type of interaction in order to obtain an analytical solution, or assume complex interactions, but not to obtain the analytical solutions. Moreover, the very possibility of the derivation of collective behavior based on even the full information about individual level interactions is in reasonable doubt (ref.).

This paper introduces a "from the middle" approach, which was initially based on two fundamental propositions of Malthus that were mentioned earlier. Here, "from the middle" means that this approach introduces an interim (between the population and individual) level of consideration. This level represents the community organization composed of diverse individuals, who are involved in one way or another in the process of sharing out of common resources. One might say that in such an approach, the variety of interactions among individuals that is highlighted by other approaches is replaced by the final result of these interactions, the distribution of resources among members of the community. Such a replacement is not a new idea; in fact, it is one of the classical methods of statistical physics, as well as the traditional way of describing competition in the economy, and yet, in the field of population dynamics, it has not received sufficient attention.

The paper suggests that the overall dynamics of the population is the accumulated result of two mutual processes occurring on different levels: survival-reproduction at the individual physiological level and the partitioning of resources at the community level. This paradigm appears to be consistent with the vision of Malthus, or at least more consistent than other paradigms, which are narrowly focused on only one level.

First, the paper intends to reconstruct a model of population dynamics that remains true to Malthus, taking into account his basic propositions, and then comparing the results of the analysis of this model with his original conclusion. Secondly, the paper adds a new proposition, which assumes that relative equality in the distribution of resources can evolve through natural selection, and introduces the community dynamics models. Finally, the paper addresses the issue of carrying capacity, and shows an example of a non-equilibrium population that has no equilibrium population size (carrying capacity), but, nonetheless, remains limited, and may exist for a long time.

The paper is organized as follows. Section 2 introduces the model of community as a system of two differential equations, where the first equation represents the dynamics of population in the case of the unequal distribution of resources, and the second equation represents how this inequality can be changed within the community. Section 3 then examines the particular cases of community-resource relationships, which lead to the equilibrium population size (carrying capacity). Section 3.1 investigates the stability of equilibrium for the previous cases, in connection with the so-called Malthusian catastrophe. Section 4 examines

the special case of community-resource relationships in which the population has no equilibrium size or carrying capacity and can demonstrate a multi-stage demographic transition. Finally, Section 5 discusses the results and suggests some conclusions.

2. Community dynamics model

This section develops the basic Conspecific Community Dynamics Model (CCDM) with which we will work in the next sections. From a mathematical point of view, the model of community dynamics is a system of equations consisting of the equation of population dynamics and the equation of organizational dynamics of community. We assume that population dynamics and organizational dynamics operate on different time scales. The population dynamics equation describes changes in community population size, subject to the stability of the organizational structure, in the short time scale (smaller than individual lifespan), whereas, the organizational dynamics equation describes the change in the organizational structure for the larger (several generations) time scale. Here, under the organizational structure, we understand some relative measure of equality (denoted as k) in the frequency distribution of individuals with different competitiveness within the community. Therefore, when the community consists of almost equal (in the sense of competitiveness) individuals, the measure of relative equality will be close to infinity, but if the community is composed of very unequal individuals, this measure will be close to zero. Here competitiveness (denoted as s and measured in the same units as the resource) is the measure of the ability of an individual to acquire a certain amount of resources (denoted as ε) in the process of sharing out resources within the community. In other words, competitiveness is the expected value of the acquired resources. In fact, in the absence of stochasticity, it is simply equal to this quantity. In addition, we can say that the organizational structure describes the equality of opportunity in obtaining some resources among individuals within the community. We assume that an individual can build up its own competitiveness during its lifetime and that the competitiveness of an individual accumulates other traits, such as age, sex, body-size, aggressiveness, etc, which can influence foraging success.

Population dynamics can be represented in the form of general balance equations: $N_{t+1} - N_t = [\overline{W}(N_t) - \overline{D}(N_t)]N_t$, where $\overline{W}(N_t)$ and $\overline{D}(N_t)$ are crude birth and death rates. These rates can be rewritten as: $\overline{W}(N_t) = bP_b$, $\overline{D}(N_t) = \delta P_s + (1 - P_s) - cP_b$, where P_b and P_s are the reproducing and surviving portions of the population, b and δ are physiological fecundity and aging mortality, c is so-called reproduction cost or additional mortality of parents. On the one hand, these fractions are functions of some arguments: $P_b(\varepsilon_b, R, N_t, k)$, $P_m(\varepsilon_m, R, N_t, k)$, where R is total resource rate, which is unequally shared among individuals within the community, and ε_b and ε_m are amounts of resources needed for reproduction and survival for one individual respectively. On the other hand, these fractions can be represented as the upper parts of cumulative distribution function of the resource distribution function $E(\varepsilon, k)$. Then suppose that this distribution is the integrated result of stochasticity in the process of resource allocation and underlying competitiveness distribution. Therefore, the resource distribution function can be decomposed as:

$$E(\varepsilon, k) = \int_0^\infty p(\varepsilon \mid s) S(s \mid k, \theta) ds \quad ,$$

where stochastic part $p(\varepsilon \mid s)$ is a conditional probability distribution that determines the chance of an individual with a value of competitiveness s for a resource in the number of ε, $S(s \mid k, \theta)$ is the distribution function of competitiveness, which depends on the parameters of

shape k and scale θ parameter. Here we assume that the competitiveness distribution is the distribution of shape-scale type, because k as a measure of relative equity among individuals must be independent of population size and total resource rate, which represents the scale of the system. Further, for ease of mathematical calculations, we assume the competitiveness distribution to be equal to gamma distribution, which also makes the interpretation of shape parameter a more familiar setting, because we can associate it with such well-known measure of inequity of resource distribution as the Gini coefficient $Gini(k) = 1 - 2I_{\frac{1}{2}}(k+1,k)$, where $I_x(a,b)$ is the regularized incomplete beta function. Note that the Gini coefficient is commonly used as an indicator of inequality in the distribution of resources, but here it is used as a measure of inequality of opportunity in obtaining resources.

Stochastic part $p(\varepsilon \mid s)$, which represents the randomness in the resource allocation process, must satisfy the following natural conditions:

1. Expectation $\bar{\varepsilon}$ is equal to s (unbiased expectations).
2. Variation $Var(\varepsilon)$ increases, while the coefficient of variation $CV(\varepsilon)$ decreases with s (high competitiveness provides a lower relative risk of extinction).

The simplest choice for such probability distribution is Poisson distribution. Because Poisson is dimensionless (count number of occurrences) we need to determine some unit (rate of Poisson distribution) with has the same dimension as s (energy content of food).

It is not a unique choice, and moreover each yields different models of foraging behavior. Here, however, for the sake of simplicity, we will consider a model with unit equal to θ. After choosing the exact form of both distributions, resource distribution can be rewritten in the form of negative binomial distribution $E(\varepsilon_\theta, k) = Negb(\varepsilon_\theta \mid k, 1/2)$, where ε_θ is resource, which is measured in θ units. By assuming that $\bar{\varepsilon} = \bar{s} \equiv R/N$ or that mean resource consumption equals to mean competitiveness and both equal to average resource per individual, we determine the scale parameter as $\theta_t = \frac{R}{kN_t}$. Then, $P_b(\varepsilon_b, R, N_t, k)$ and $P_m(\varepsilon_m, R, N_t, k)$, which are upper parts of cumulative resource distribution can be calculated as $I_{\frac{1}{2}}\left(\frac{k\varepsilon_b N_t}{R}+1, k\right)$ and $I_{\frac{1}{2}}\left(\frac{k\varepsilon_m N_t}{R}+1, k\right)$. After substitution of these fractions into balance equation, we get:

$$N_{t+1} = \left((b-c)I_{\frac{1}{2}}\left(\frac{k\varepsilon_b N_t}{R}+1, k\right) + (1-\delta)I_{\frac{1}{2}}\left(\frac{k\varepsilon_m N_t}{R}+1, k\right)\right)N_t \quad (1)$$

Equation (1) always has a positive net growth rate, because c (specific mortality of parents) cannot exceed b (fecundity), which simply means that it is not possible to give a birth less than one offspring. As well, δ (aging mortality) cannot exceed one, which means that it is not possible to die more than one times. This equation can be formally approximated as a differential equation, it is necessary to fix the time interval to zero, and replace the identified time interval parameters (all parameters, except for k) with their corresponding instant rates. For the convenience of recording, we will keep the same symbols for the parameters that were used previously. However, it will be kept in mind that, in the differential equation, these parameters have a sense of instant rates, and after rewriting, we get:

$$\dot{N} = \left((b-c)I_{\frac{1}{2}}\left(\frac{k\varepsilon_b N}{R}+1, k\right) + (1-\delta)I_{\frac{1}{2}}\left(\frac{k\varepsilon_m N}{R}+1, k\right) - 1\right)N \quad (2)$$

Therefore, we have the equation of population dynamics, in which crude birth and death rates are not only functions of population density, but also rather functions of physiological parameters and parameter of equality k. Further, we will use this aspect in order to track changing demographic parameters as a response to the organizational structure change.

Suppose now that parameter k can be slowly evolved under selection for competitiveness. The simple logic behind this assumption is that individuals that are more competitive can produce more offspring, and if competitiveness can be inherited in some or other way, future generations will include more and more individuals that can achieve the same high competitive positions as their parents occupy. In turn, difference in competitiveness composition between generations produces selection pressure on organizational structure, which reacts to this pressure so that the shifting values of k in such a way as to reduce this pressure, or that the same thing towards greater conformity with the new generation competitiveness composition. As a result, this process leads to the fact that the distribution of opportunities for obtaining resources become more even, which means an increase in the value of k. Next, we formalize this intuition in the form of the equation for the organizational dynamics.

We begin with quasi-replicator equation: $\frac{d}{dt}S(s) = hS(s)(W(s) - \overline{W})$, which differs from the standard replicator equation only by a factor of heredity $h << 1$. This difference arises because the offspring do not directly inherit the competitiveness of their parents, but are rather more likely to build their competitiveness to the level of the parents during their lifetime. "Fitness" $W(s)$ can be calculated as the expected number of offspring of one individual, depending on its competitiveness as: $W(s) = bPoisson(\varepsilon_\theta > \varepsilon_b / \theta \mid s)$, where $Poisson(\varepsilon_\theta > \varepsilon_b / \theta \mid s)$ denotes the Poisson cumulative distribution, which determines the probability of obtaining sufficient quantities of resources, for reproduction for an individual with a given competitiveness. "Fitness" $W(s)$ here is not individual fitness in the classic (genetic) sense, because it is tied to the competitiveness of an individual rather than to the individual itself. In other words, we consider the co-selection, where the number of offspring depends on the ability of the individual to take a favorite position in the community, which strongly depends on the abilities and numbers of other members of the same community. Further, the left-hand side of the equation can be rewritten as:

$$\frac{d}{dt}S(s) = \left(\frac{\partial S(k,\theta(k))}{\partial k} + \frac{\partial S(k,\theta(k))}{\partial \theta}\frac{\partial \theta}{\partial k}\right)\dot{k} = a(s,k)\dot{k}$$

Then, after averaging both sides of the quasi-replicator equation for s we get:

$$\dot{k} = h\overline{A}(k)[\overline{w}(k) - \overline{W}(k)\overline{s}(k)],$$

where $\overline{w}(k) = \int_0^\infty sW(s)S(s)ds$, $\overline{s}(k) = R/N(k)$ and $\overline{A}(k) = 1/\int_0^\infty sa(s,k)S(s)ds$.

Unfortunately, to obtain an exact analytical solution of this equation is quite difficult, but for each special case and some range of parameters, one can make a rough estimate. In our case, for k not to fall too close to zero, an approximate equation can be evaluated as:

$$\dot{k} = Ahk^{-\gamma}, \qquad (3)$$

where $\dot{k} << \dot{N}$ is a necessary condition for the timescales separation, $A > 0$, $\gamma > 1$ are some of the coefficients that are dependent on other parameters.

Equations (2) and (3) complete the mathematical formulation of the model, the equation (3) for the organizational structure dynamics can be solved easily, the specific solution is:

$$k(t) = \left[Ah(1+\gamma)t + k_0^{1+\gamma}\right]^{\frac{1}{1+\gamma}} \quad , \tag{4}$$

where $k_0 = k(t_0)$ is the initial value of k. This solution provides a basic understanding of the dynamics of organizational structure: Firstly, the distribution of opportunities to obtain resources, and with it the distribution of this resources, is always changing to a more even ($k(t_2) > k(t_1)$ if $t_2 > t_1$). Secondly, the speed of these changes is always decreasing ($\dot{k}(t_2) < \dot{k}(t_1)$ if $t_2 > t_1$). In the next sections, we will investigate the behavior of the population size of the community at large time scales, depending on k, realizing that with the help of the solution (4), a direct dependence on time can be obtained.

3. Carrying capacity

In this section, we will consider two cases of interaction between community and resources that lead to the existence of some equilibrium value of the population size (carrying capacity).

In the first case, the population will have no effect on the overall resource rate R and the resource itself will remain constant and finite. The population equation for this case equals to the equation (2). It has the following basic properties: while the inequality $(b - c - \delta + 1)I_{1/2}(1, k) > 1$ holds, the equation (2) has one fixed point $\hat{N}(k)$ different from zero. From the perspective of a large time scale, we can say that this fixed point represents an instant carrying capacity of population $\hat{N}(k) \equiv K(k(t))$, which slowly evolves under the organizational change (Fig.1). Perhaps the main feature of $K(k(t))$ behavior is the fact that it quickly reaches a maximum at a certain point $k_{\max}$ and then slowly decreases to asymptotic value R/ε_b. That is, in the community there is an optimal level of equality that provides the maximization of population size under conditions of resource limitation.

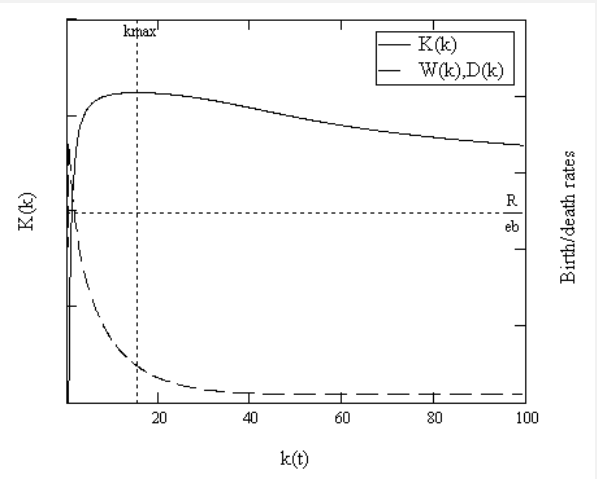

Figure 1| Finite constant resource. The instant carrying capacity $K(k)$, the reproduction $\overline{W}(k)$ and mortality $\overline{D}(k)$ rates depending on the organizational structure changes $k(t)$ (the shape parameter of the competitiveness distribution), in case of fixed resources.

In the second case, we assume a potentially infinite amount of resources, but the ability of the community to extract these resources will be declining along with the growth in the population.

This case, in the broadest sense, can be regarded as a model for Malthus's law of growth, because the main statement "the population is growing exponentially, while the subsistence increases linearly" can be reformulated as, "the total amount received by community resources grows logarithmically with population growth". Therefore, we can rewrite Malthus's law in the form: $R(N) = R_0 \ln(N+1)$ or in the equivalent form of marginal contribution of each additional individual in the community resources:

$MR(N) = \frac{\partial R(N)}{\partial N} = \frac{R_0}{N+1}$, where R_0 is an intrinsic contribution of an individual. The population dynamics equation (2) in this case can be rewritten as

$\dot{N} = \alpha(N,k)N$, where $\alpha(N,k)$ is so-called Malthusian parameter, which equals to

$$\alpha(N,k) = (b-c)I_{\frac{1}{2}}\left(\frac{k\varepsilon_b N}{R_0 \ln(N+1)} + 1, k\right) + (1-\delta)I_{\frac{1}{2}}\left(\frac{k\varepsilon_m N}{R_0 \ln(N+1)} + 1, k\right) - 1 \qquad (5)$$

The equation (5) has one nontrivial fixed point, while condition

$(b-c)I_{\frac{1}{2}}\left(\frac{k\varepsilon_b}{R_0} + 1, k\right) + (1-\delta)I_{\frac{1}{2}}\left(\frac{k\varepsilon_m}{R_0} + 1, k\right) > 1$ holds. In general, the behavior of the instant carrying capacity $K(k(t))$ in this case is similar to the previous case (Fig.2). It asymptotically seeks to $K_\infty \xrightarrow[t\to\infty]{} -\frac{R_0}{\varepsilon_b} W\left(-1, -\frac{\varepsilon_b}{R_0}\exp\left(-\frac{\varepsilon_b}{R_0}\right)\right) - 1$, where $W(x,y)$ is a Lambert function.

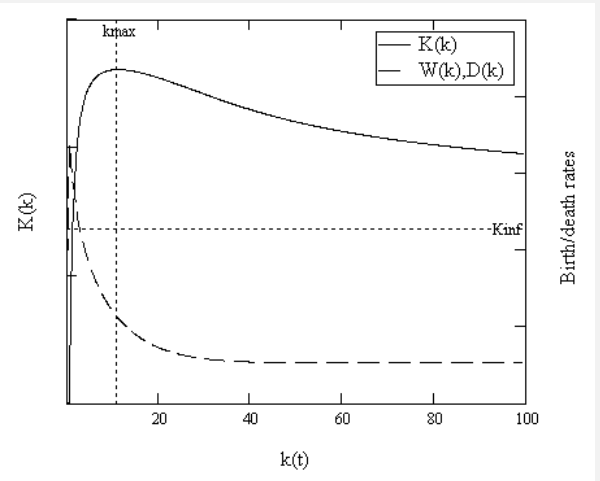

Figure 2| Infinite resource, diminishing marginal contribution. The instant carrying capacity $K(k)$, the reproduction $\overline{W}(k)$ and mortality $\overline{D}(k)$ rates depending on the organizational structure changes $k(t)$, in case of the diminishing marginal contribution.

In both cases, the rate of reproduction $\overline{W}(k(t))$ and mortality $\overline{D}(k(t))$ rates equal each other, because the community is in equilibrium. However, in the long term, these demographic parameters are undergoing a transition towards a reduction up to the level of aging mortality

(Fig.1, Fig.2). One might say that such communities evolve in the direction of increasing life expectancy, but not an increase in population size.

The model demonstrates the so-called "demographic-economic paradox", namely, the inverse relationship between fertility and the average per capita amount of resource (Fig.3). It also predicts the existence of other aspects of such a relationship, where the decreasing of fertility coincides with the decreasing of average per capita amount of resource. It is a little surprising that such a "paradox" can be explained on the basis of the fundamental principles proposed by Malthus, and one additional assumption about organizational changes.

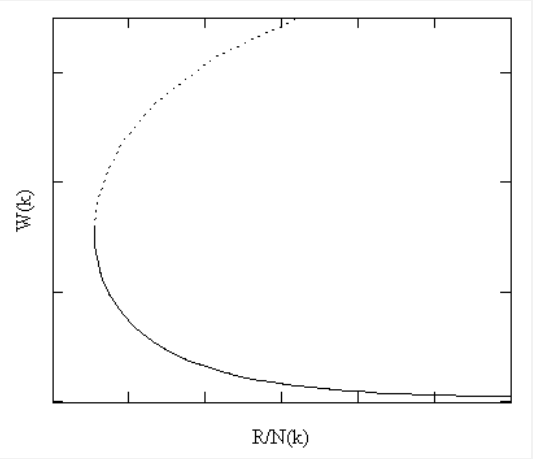

Figure 3| "Demographic-economic paradox". Starting from the $k_{\max}$, the birth rate $\overline{W}(k)$ is inversely related to the average per individual amount of resource.

It can be shown that all communities that exhibit the diminishing marginal contribution also have the instant carrying capacity, in spite of the potentially unlimited amount of resources. In this sense, the case of unlimited resources does not much differ from that of limited resources, because in both cases the population has the carrying capacity. Therefore, it can be concluded that the amount of resources itself is not a limited factor for the population growth; instead, population growth is limited by ability of the community to extract resources, which can be represented by the marginal contribution function. If this function diminishes along with the population size, then the population remains limited regardless of the amount of available resources. Malthus did not explicitly express this conclusion, but his reasoning on the diminishing (along with population size) productivity of land tenure allows one to suggest that he had it mind. In turn, it reassures us that this math model captures his idea.

3.1 Malthusian catastrophe (supplementary section)

Modeling of Malthus's thoughts will not be complete without a mention of his vision of the issue of population regulation. He suggested that an unchecked population outgrows its ability to provide subsistence, which leads to starvation or even extinction. We can say that he suspects that unchecked population is regulated through the overpopulation-starvation cycle. He also suggested that this cycle could be so severe as to threaten populations in the form of a catastrophe. In order to distinguish the different situations, we introduce two types of Malthusian catastrophes. The first type of Malthusian catastrophe assumes that the cycle of overpopulation-starvation is restricted within certain limits, and therefore cannot directly lead

to extinction, whereas the second type of Malthusian catastrophe involves the cycle of unlimited amplitude, which may lead to extinction. In the previous section, we use the community model in the form of a differential equation, which always gives a stable equilibrium. In this section, we return to the difference equation form (1) in order to investigate the properties of stability. In the difference equations, fixed point $K(k)$ loses its stability, if the first derivative $\left.\frac{\partial(\alpha(N,k)N)}{\partial N}\right|_{N=K}$ in the fixed point becomes less than minus two.

It can be shown that a community with a carrying capacity depending on the parameters can demonstrate the following four types of the population behavior with increasing $k(t)$:

1. Be stable up to some large value of k, then undergo Malthusian catastrophe of the first type.
2. Be stable up to some large value of k, then undergo Malthusian catastrophe of the second type, and become extinct.
3. Be stable up to some moderate value of k, then undergo Malthusian catastrophe of the first type, and then re-establish stability at some interval of k and then undergo Malthusian catastrophe of the second type, and become extinct.
4. Be stable up to some moderate value of k, then undergo Malthusian catastrophe of the second type and become extinct.

Generally, the equilibrium population size always loses stability at sufficiently big value of k and may lose stability around the maximal population size point $k_{\max}$. While $k(t) \to \infty$, the community undergoes Malthusian catastrophe of the second type and becomes extinct if

$b > c + (1-\sigma)\left(\frac{K_m}{K_\infty} - 1\right)$, where $K_m = -\frac{R_0}{\varepsilon_m} W\left(-1, -\frac{\varepsilon_m}{R_0}\exp\left(-\frac{\varepsilon_m}{R_0}\right)\right) - 1$, is fulfilled. Otherwise, the community undergoes Malthusian catastrophe of the first type and the population size varies between $(1-\sigma)K_\infty$ and $(b-c-\sigma+1)K_\infty$ values.

Comparing Malthus's conclusion and the result of the math model, which models his thoughts, we can note some ambiguity. On the one hand, in the long run, conclusions are consistent and the unchecked population inevitably finds itself involved in the overpopulation-starvation cycle and may become extinct if fecundity is sufficiently high. On the other hand, in the short run, the unchecked population can be very stable and successfully regulate itself. This discrepancy probably emerges because Malthus did not consider the organizational changes and was forced to make a general conclusion based on a choice between long-term and short-term dynamics as alternatives. The community dynamics model considers both time scales, and can accordingly draw conclusions on the basis of it. Therefore, the stability of unchecked population is a matter of time scale.

4. Beyond of the carrying capacity

In previous sections, we consider a situation in which the marginal contribution diminishes with the population size. Here we consider a situation in which the marginal contribution remains constant $MR(N) = R_0$. Interestingly, this assumption was dominant until the time of Malthus's work (Condorcet, *Sketch for a historical picture of the progress of the human spirit*, 1774) and Malthus himself strongly opposed it. (The first edition of *The Principle of Population* was largely devoted to criticism of this idea.) Indeed, it means that resources can

grow at the same rate as the population (i.e. exponentially), which leads to population explosion (unlimited growth), as Malthus claimed. Here we will show that Malthus was not accurate in its criticism, and a resource that is growing at the same rate as the population does not necessarily lead to an infinite size of the population. The key point, which was not considered them, is that the community itself can evolve towards a more equitable redistribution of resources, which, in turn, could reverse the growth of the population.

Suppose that the marginal contribution is constant or that community resources grow linearly with population: $R(N) = R_0 N$ .Thus, population dynamics equation (2) can be rewritten as:

$$\dot{N} = \alpha(k)N \quad , \tag{6}$$

where Malthusian parameter $\alpha(k)$ does not depend on the population size:

$$\alpha(k) = (b-c)I_{\frac{1}{2}}\left(\frac{k\varepsilon_b}{R_0}+1,k\right)+(1-\delta)I_{\frac{1}{2}}\left(\frac{k\varepsilon_m}{R_0}+1,k\right)-1$$

It is easy to see that such a population has no nontrivial fixed points (equilibriums) or carrying capacity and, depending on the sign of $\alpha(k)$ can only exponentially grow or decline, as it states in Malthus's law. However, in the long term, population dynamics is determined by the organizational dynamics that can change the sign of a Malthusian parameter, and accordingly reverse population growth.

Due to the absence of instant carrying capacity, eventually the population can either increase to infinity or become extinct. The main variables that determine the final state are $R_0, \varepsilon_b, \varepsilon_m$. Depending on their relationship, there may be three different situations:

(1) $R_0 \geq \varepsilon_b$, when the marginal contribution provides sufficient resources for the reproduction of the individual,

(2) $R_0 < \varepsilon_m$, when this contribution is not enough even for the survival of one individual, and

(3) $\varepsilon_b > R_0 > \varepsilon_m$, when this contribution is enough for the survival, but not enough for reproduction.

In all cases, sufficiently large fecundity may lead to exponential (with variable rate) growth of the population, at a certain k interval (Fig.4). However, if we assume that organizational changes lead to a more equitable distribution of resources (to bigger k), the final state will depend on the sign of $\lim_{k\to\infty}\alpha(k)$. In the first case, $\lim_{k\to\infty}\alpha(k) = b-c-\delta$ the population grows to infinity, while the $b > c+\delta$ is fulfilled; in the second case, $\lim_{k\to\infty}\alpha(k) = -1$ the population eventually becomes extinct due to starvation; in the third case, $\lim_{k\to\infty}\alpha(k) = -\delta$ the population also eventually becomes extinct due to aging without reproduction. Note that in the second and third cases, the population could grow before the beginning of extinction, and extinction itself can take very long because the rate of organizational change is slowing over time. The statement that the population can grow even if the individual does not cover the cost of its own survival (the second case), seems strange at first glance, but here we are dealing with a community consisting of unequal individuals, and the reallocation of resources allows the population to grow.

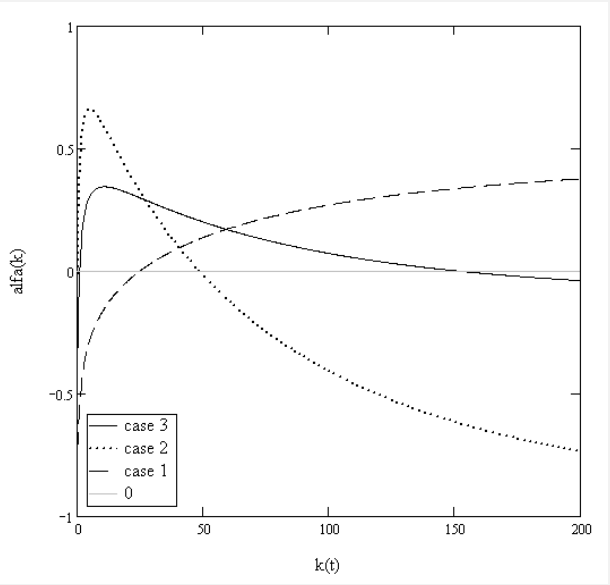

Figure 4| Population growth rate. Malthusian parameter $\alpha(k)$ depending on the organizational structure changes. The case1 $R_0 \geq \varepsilon_b$, the case2 $R_0 < \varepsilon_m$, the case3 $\varepsilon_b > R_0 > \varepsilon_m$.

A parametric solution for the population size can be obtained by solving the equation (6) for variable $k(t)$.

$\frac{1}{N}\frac{\partial N}{\partial t} = \frac{1}{N}\frac{\partial N}{\partial k}\frac{\partial k}{\partial t} = \alpha(k)$, has the specific solution $N(k) = N(k_0)\exp\left(\int_{k_0}^{k}\frac{\alpha(k)}{\dot{k}(k)}dk\right)$

where $k_0 = k(t_0)$ is value of k at the initial moment. Then we can substitute the $\dot{k}(k)$ and $k(t)$ on their explicit forms, which can be obtained by solving the organizational dynamics equation (3), and finally getting:

$$N(t) = N(t_0)\exp\left(\frac{1}{Ah}\int_{k_0}^{k(t)}\alpha(k(t))k(t)^{\gamma}\,dk(t)\right), \quad (7)$$

where $k(t) = \left[Ah(1+\gamma)t + k_0^{1+\gamma}\right]^{\frac{1}{1+\gamma}}$

For the second and the third cases, extinction time (a community lifespan) T_{ex} and a maximal population size $N_{\max}$ can be roughly estimated as:

$$T_{ex} \approx \frac{k_{ex}^{1+\gamma}}{Ah(1+\gamma)}, \quad (8)$$

where $k_0 << 1$, $\alpha(k_0) > 0$ and k_{ex} is the solution of equitation: $\int_0^k \alpha(k)k^{\gamma}dk \equiv 0$

$$N_{\max} \approx \exp\left(\frac{1}{Ah}\int_0^{k_m}\alpha(k)k^{\gamma}dk\right), \quad (9)$$

where k_m is the solution of equation $\alpha(k) \equiv 0$.

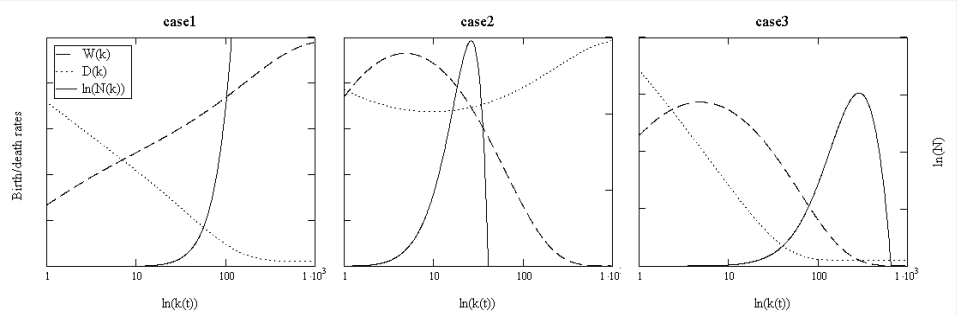

Figure 5| Three types of the population growth. The population size $N(k)$, the reproduction $\overline{W}(k)$ and mortality $\overline{D}(k)$ rates depending on the organizational structure changes $k(t)$ for three cases.

The community without the carrying capacity demonstrates a varied behavior of demographic parameters (fig.5). For instance, in the third case, the demographic transition process can be divided on six stages (fig.6):

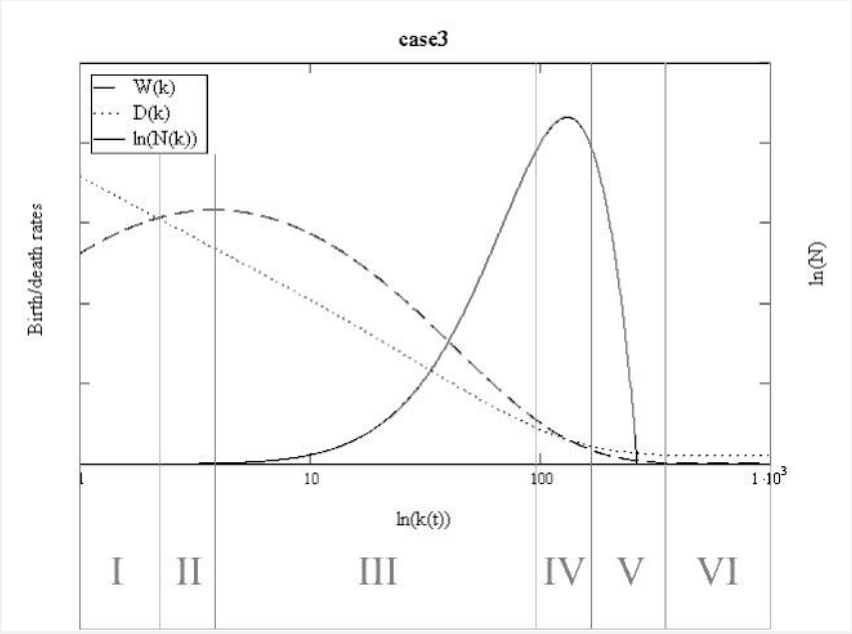

Figure 6| Demographic transition. Six stages of the demographic transition in case 3.

Stage I, where death rates and birth rates are both high and almost equal, the population barely survives. Stage II, where death rates fall, while birth rates increase up to some maximal value. Stage III, where birth rates start to decline, while death rates also decline. Stage IV,

where death rates and birth rates are both low and almost equal, and the population size reaches maximal value at this stage. Stage V, where birth rates become less than death rates and the population size declines with accelerated rate. Stage VI (optional on parameters), where net rates remain negative, but start to increase and the population size declines with slowed rate. In the boundary between Stage I and Stage II, as well as in Stage IV, where death rates and birth rates are almost equal, the community without the carrying capacity can be look like as community with the carrying capacity. It is interesting that our pure mathematical model, which based on basic assumptions, gives quite similar results as the demographic transition model (Caldwell et. all 2006), which based on empirical data.
Based on the analysis of this model, it can be concluded that the community, at least in principle, can regulate itself through organizational dynamics. Here, natural selection through organizational dynamics plays the role of a limiting factor for the population growth. Perhaps it is an unusual effect of natural selection, which on the one hand favors individuals with a greater number of offspring and on the other hand limits the size of community.

In other words, the principle of "survival of the fittest" also has a reverse side, and ultimately leads to "extinction of the equally fittest".

5. Summary and conclusions

This paper adapts the basic Malthusian postulates for the analysis of population growth under natural selection. It shows that the limitation of growth should not necessarily be the result of resource scarcity. Instead, the limitation of growth may be the result of natural selection itself, which changes the organizational structure of the community towards the equalization of differences among individuals. This view of population growth as a non-equilibrium process appears to be useful in the understanding of the life-history traits dynamics.

What is surprising about this analysis is that it is quite simple, in the sense that it is based only on the obvious tenets; nevertheless, it is able to explain such complex phenomena as demographic transition and the demographic-economic paradox, which, in the opinion of some authors (Vining, D.R., 1986), is "the ultimate challenge to evolutionary approaches to human behavior". The paper shows that a decrease in the overall birth rate accompanied by an increase of the average per individual resource is not a paradox (in the sense that such a situation does not violate the postulate of Malthus), but is a direct consequence of changes in equality between individuals under co-selection process. The origin of the paradox comes from neglect of the issue of inequality between individuals, where the *average per individual* resource is assumed to be the resource that *each individual* obtains. In other words, the paradox arises when the Malthusian postulates relating to each individual are uncritically applied to a virtual "average individual". This example shows how important it is to take into account inequality among individuals in population-based studies, because there may otherwise be a pseudo-paradox like this one. This result is important also because several decades have been spent on the search for evolutionary explanations for the demographic transition phenomenon (M. B. Mulder, 1998). Unfortunately, this quest originally started from the idea of the existence of such paradox. Correspondingly, answers were sought among the various behavioral mechanisms that are far from the basic tenets of Malthus. This study shows that the demographic transition can have a simple biological explanation, which does not require additional behavioral hypotheses. We suppose that the CCDM approach can provide an analytical platform for modeling of such unstable demographic processes.

6. Acknowledgments

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III

Shoal-based approach to fish population dynamics

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Abstract

"Fishes used to live under water. Fishes are not a floating biomass. Fishes differ among themselves, and not only in their taxonomical affiliation, sex, and age. Fishes need certain amount of food for survival and reproduction. Fishes used to live into groups. Fishes used to live in stochastic environment."- This is a list of basic facts that are still barely considered together, if at all, in models of fish population. The newly developed Conspecific Community Dynamics Model (CCDM) approach, in combination with optimal shoaling models (OSM) allows the taking into account of these facts and offers an analytical shoal-based model for fish population dynamics. This model provides convenient tools for investigating such issues as a density-dependence and bi-stability. The model gives insight into how species-specific physiology, involvement in shoaling behavior, resource availability and cannibalism affect fish population dynamics.

Key words: fish ecology, fish population dynamics, optimal foraging theory, shoaling behavior, hydrodynamic efficiency, density-dependence, bi-stability,

1. Introduction

It has been widely recognized that defense against predators, enhanced foraging success, and higher success in finding a mate are major factors that can explain shoaling behavior. It also has been suggested that fish benefit from shoal membership through increased hydrodynamic efficiency. Nonetheless, decreasing individual energy spent on locomotion in a shoal as a cause of agglomeration has received relatively little attention (compared to others factors) from fish ecological theory. The main reason for this neglect seems to be that it has appeared difficult to deal with shoal behavior in the context of individual energy spending in classical fish population model frameworks, which do not explicitly include individual physiology and resources. We use the CCDM approach [20], which explicitly includes these aspects and allows for the taking into consideration of details of shoaling behavior.

Different fish species demonstrate a wide variety of collective behavior, from occasional shoaling in multi-species groups to constant schooling in conspecific cohorts. Moreover, within one species, spatial formation, distribution of body-sizes, instant shoal size and speed of shoal are constantly changing. Nevertheless, despite such complexity, we suggest that the inclusion of the effect of reducing hydrodynamic drag can be the basis for understanding the general aspects of shoaling behavior. This is because, unlike other factors such as defense against predators, enhanced foraging success and higher success in finding a mate, individual fish can instantly benefit from membership in the community by reducing their energy costs on the locomotion [6-11].

Experimental studies of fish locomotion [3-4] suggest that swimming fish generate a complex hydrodynamic structure, known as reverse von Karman street, which is composed of vortices with interspersed jet flow oriented downstream. Other fish following behind can effectively use this "curved street" to reduce their own energy expenditure if they have a similar body-size and muscle structure. It may explain why fish tend to swim behind other fish that resembles itself. It is also important to note that research in the field of hydrodynamics [23] shows that the utilization of the effect of reducing hydrodynamic drag requires extraordinary abilities of the individual. At least it should have a unique ability to respond instantaneously and interactively to small changes in the basic flow, which is impossible without the presence of special sense organs. It is not surprising that such a special organ – a lateral line – is present in many fish species. This fact can be interpreted as evolutionary evidence of exceptional importance of collective behavior in the aquatic environment. We argue that the direct and instant benefit that provides hydrodynamic efficiency for each shoal member should be considered as fundamental, while other factors be considered important. Since the lateral line in some sense represents the inner ear (contains neuromasts similar to those that have the ears of vertebrates), the movement of fish within the shoal can be compared to singing in the choir, where each individual hears the vibration caused by others and adapts its vibration in unison.

Here we develop an optimal shoaling model (OSM), which is a form of optimal foraging theory (OFT) [1-2]. It supposes that individual fish within shoals forage in such a way as to maximize their effective energy consumption per unit time. In turn, the effective energy consumption represents the tradeoff between the energy expended on the locomotion and the energy obtained from food, and can be calculated as:

$$R = \rho SL - g(v) f(c) SL \ , \qquad (1)$$

where ρ is volume density of food (measured in energy units), c is length of shoal along velocity vector $\vec{v}$, S is cross section area and $L = \int_0^\tau v(t)dt$ is covering during period τ distance. Further, $g(v)$ is friction force for one fish (approximately, $g(v) \approx v^2$ for $\mathrm{Re} > 1$ and $g(v) \approx v$ for $\mathrm{Re} < 1$) and $f(c)$ is some increasing function, which represents the effect of reduction of drag for fish that move close behind other fish. As first approximation, it can be assumed that $f(c) \approx c^\alpha$, where α is positive and less than one ($\alpha = 1$ means an absence of reduction effect). This tradeoff strongly depends on the density of resources. Therefore, optimal shoal behavior may be to switch between different types depending of food availability. There are three different temporal types of spatial formation: (i) traveling formation provides the least energy spending on the relocation. It is optimal for migration to spawning area, as well as for migration between feeding grounds. (ii) Resting formation ensures absolute minimization of energy consumption on locomotion, but does not allow any relocation or foraging. It is optimal in the case of rest or protection against predators. (iii) Foraging formation maximizes the consumption of food. It is optimal where there is a high concentration of food.

The first formation promotes shapes with long c in which S depends on body-size distribution only, because individual fish can fully exploit the effect of drag reduction only if they follow behind fish of the same size (Fig.1a). The second formation promotes torus shape (fish school), where all fish, not only followers, can use drag reduction effect, and which is thus the most energy efficient shoal formation (Fig.1b). In contrast, the third formation promotes a shape with greater S, simply because it provides the biggest search area and consequently biggest energy consumption (Fig.1c).

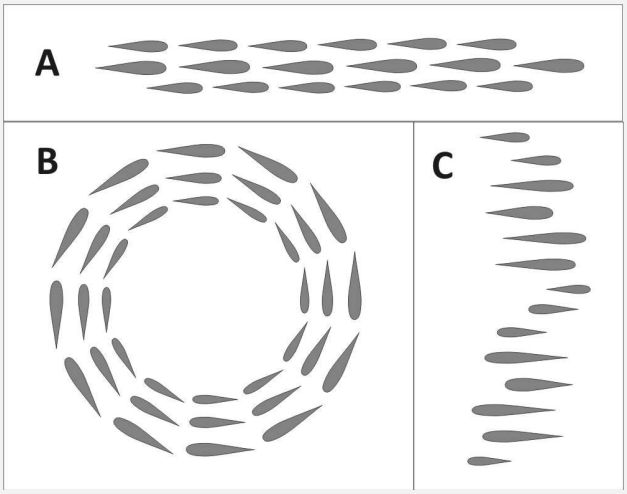

Figure 1| Spatial shoal formation: (a) traveling formation, (b) resting formation and (c) foraging formation.

Generally, we assume that types of shoal formation switch from one to another and depend on local food density and shoal satiation, but, on average, a tradeoff between foraging and movement takes place. This depends on the numbers of fish in the shoal (Fig. 2). Consider some average speed $\bar{v}$, average food density $\bar{\rho}$ and average $\bar{c}, \bar{S}$, we can suppose that $\bar{c} \approx N^{1/3}$, $\bar{S} \approx N^{2/3}$, $\tau \equiv 1$ and rewrite (1) as

$$R(N) = N^{2/3}(A(\bar{\rho})\bar{v} - B(\bar{v})N^{\alpha/3}), \qquad (2)$$

where $A(\bar{\rho}), B(\bar{v})$ are some increasing functions of their arguments. Then we can find optimal shoal size N_{opt} (at this size the shoal reaches maximal effective energy consumption) and N_0 is maximal shoal size (at this size effective energy consumption becomes negative).

$$N_{opt} = \left(\frac{2}{2+\alpha}\right)^{3/\alpha} N_0 \ , \ N_0 = \left(\frac{A(\bar{\rho})\bar{v}}{B(\bar{v})}\right)^{3/\alpha} \qquad (3)$$

The relative strength of the effect of hydrodynamic efficiency can be defined as the value of the second derivative at the optimum shoal size

$$\frac{\partial^2}{\partial N^2} R(N)\Big|_{N=N_{opt}} = -\frac{1}{9N_{opt}^{\ 4/3}}\left(2A(\bar{\rho})\bar{v} - (2-\alpha-\alpha^2)B(\bar{v})N_{opt}^{\ \alpha/3}\right) \qquad (4)$$

Equation (2) sets up the relation between optimal and maximal shoal sizes on the one hand and food density and shoal speed on the other. For slow motion with $\mathrm{Re} < 1$ and $B(\bar{v}) \approx \bar{v}$, maximal and optimal shoal size depends on food density only. This means that swarm size of small body-size fish species, as well as larvae, depends on local food density entirely. In distinction, for most adult fish $\mathrm{Re} > 1$ and $B(\bar{v}) \approx \bar{v}^2$, and thus increase of speed has a negative effect on both maximal and optimal shoal size.

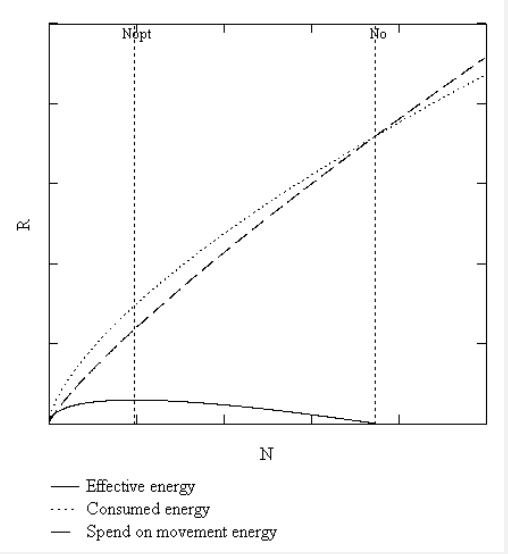

Figure 2| Tradeoff between energy consumed and spent on locomotion.

Based on OST we can draw some preliminary conclusions. Involvement in shoaling behavior depends strongly on the typical distance this fish species migrates. Species that migrate long distances have a greater influence on the hydrodynamic efficiency and are forced to coalesce into a similar body-size, conspecific cohorts of a certain size, because otherwise the spending on locomotion can be unsustainable. Examples of such species may be herring and tuna, which spend almost all the time in the permanent migration within similar body-size, conspecific cohorts. Other species that migrate only during the spawning season may form non-permanent groups that are not so demanding in terms of the composition and size of cohorts. Next, we will show how involvement in collective behavior can fundamentally affect the type of population dynamics.

2. Shoal-based population dynamics model

Here, for illustration purposes, we will use the simple version of the CCDM model [20-22], which assumes the following: (i) Distribution of the competitiveness has the form of Gamma distribution. (ii) Stochasticity of resource distribution has the form of Poisson distribution. (iii) Physiological response functions are nutrition-dependent and have "caricature" one-step shape, which means that the individual can survive only if it acquired more than ε_m amount of resources, the individual can reproduce only if it acquired more than ε_b ($\varepsilon_b > \varepsilon_m$) resources and the individual has an aging mortality rate δ and constant fecundity rate b. (iv) Total resources (effective energy consumption) available for the community depend on shoal size according to equation (2). These assumptions allow us to get the next population dynamics equations

$$N_{t+1} = \left(bI_{\frac{1}{2}}\left(\frac{k\varepsilon_b N_t}{R(N_t)} + 1, k \right) + (1-\delta) I_{\frac{1}{2}}\left(\frac{k\varepsilon_m N_t}{R(N_t)} + 1, k \right) \right) N_t \ , \qquad (5)$$

where $I_x(a,b)$ is regularized incomplete beta function, and k is shape parameter of competitiveness distribution that characterizes the level of equality within the shoal. Species that tend to organize themselves into similar body-size, conspecific cohorts, presumably have greater values of k than species that are less involved in shoaling behavior. Depending on values of k and differences between ε_b and ε_m, equation (5) shows various types of density-dependence (Fig. 3.).

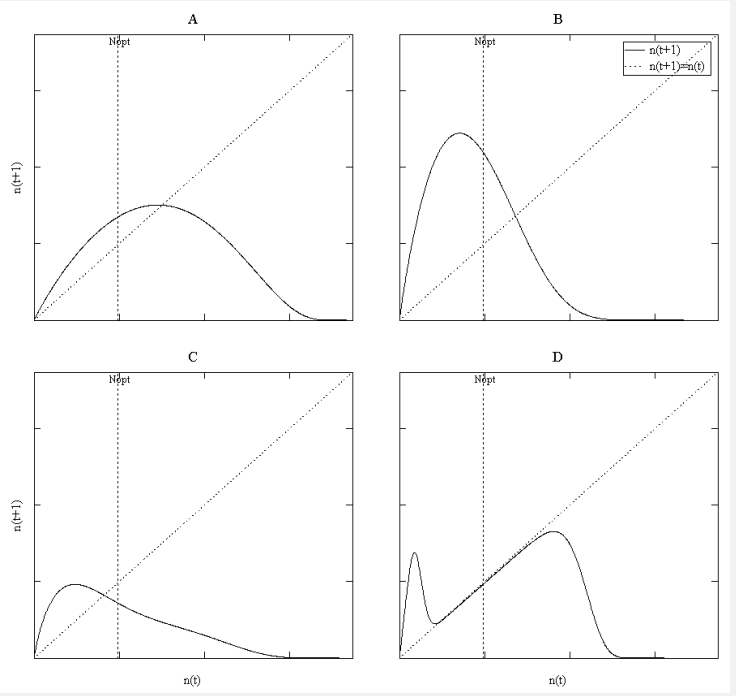

Figure 3| $N_{t+1}(N_t)$ **plots of equation (5) for different sets of parameters:** (A) logistic type of density dependence, (B) Moran-Ricker type, (C) Maynard-Smith-Slatkin type and (D) "standard empirical" type.

For $\varepsilon_b \approx \varepsilon_m$ and small k equation (5) gives close to logistic model result (Fig. 3.a), whereas for intermediate range of k it can be approximated by classic Moran-Ricker model [12,15] (Fig. 3.b). In case of $\varepsilon_b > \varepsilon_m$ and small k equation (5) gives close to Maynard-Smith-Slatkin model [13-14] result (Fig. 3.c). Therefore, shoal-based models include basic fishery population models as special cases. At first glance at the values $\varepsilon_b > \varepsilon_m$ and sufficiently large k there is an unfamiliar relationship (figure 3.d). However, if we rewrite equation (5) in terms of recruitment and survival

$$recruitment(N_t) = bI_{\frac{1}{2}}\left(\frac{k\varepsilon_b N_t}{R(N_t)} + 1, k\right)N_t$$

$$survival(N_t) = (1-\delta)I_{\frac{1}{2}}\left(\frac{k\varepsilon_m N_t}{R(N_t)} + 1, k\right)N_t \qquad (6)$$

$$N_{t+1} = recruitment(N_t) + survival(N_t)$$

then you can recognize one of the most standard empirical models of the fish population dynamics (Fig. 4.). Near the point of equilibrium $\hat{N}$, this equation can approximate as

$$recruitment(N_t) \propto Moran\_Ricke(N_t)$$
$$survival(N_t) \propto (1-\delta)N_t \qquad (7)$$

in which case it becomes exactly equal to the standard empirical models. Such an exact match, in a sense, can be regarded as strong empirical evidence in favor of the shoal-based model. It should be noted that shoal-based model is derived from first principles such as the necessity of food for survival and reproduction, inequality among fishes within shoal and collective nature of foraging. Next, we elaborate further on the issue of density-dependence.

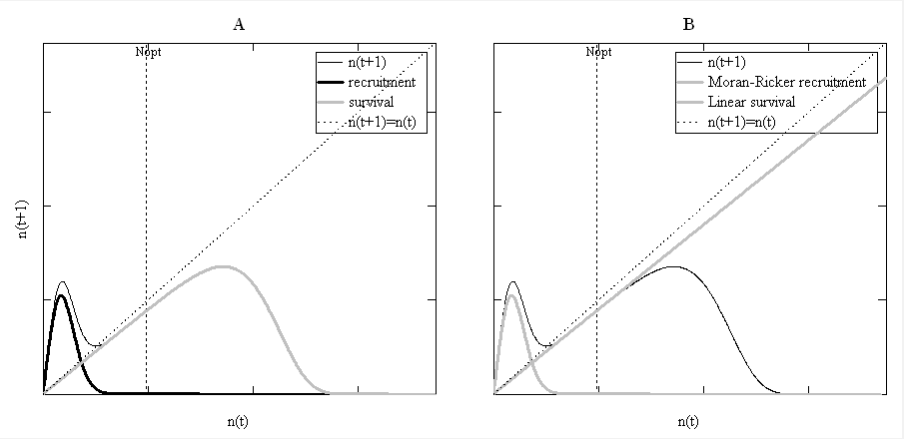

Figure 4| Comparison of the shoal-based model and the standard empirical model. (A) Decomposition of the shoal-based model on recruitment and survival parts. (B) Approximation of the shoal-based model by Moran-Ricker recruitment function and linear survival function.

3. Density-dependence

The analysis of the shoal-based model shows that the density-dependence is essentially different for different intervals of shoal size. There are two thresholds and three characteristic intervals. The first threshold is $N_R = \frac{R(\hat{N})}{\varepsilon_b}$, and it can be called a recruitment-threshold, shoal size below which leads to mass spawning and recruitment. The second threshold is $N_S = \frac{R(\hat{N})}{\varepsilon_m}$, and it can be called a starvation-threshold, shoal size above which leads to mass starvation. There are three characteristic intervals of the density-dependence: (i) on the

interval from 0 to about N_R there is some density-independent with significant positive net growth rate. (ii) On the interval from about N_R to about N_S there is some weak density-dependence at small negative net growth rate. (iii) On the interval from about N_S to ∞ weak density-dependence is also observed, along with a significant negative net growth rate. Accordingly, a strong density-dependence is observed only near thresholds (Fig. 5).

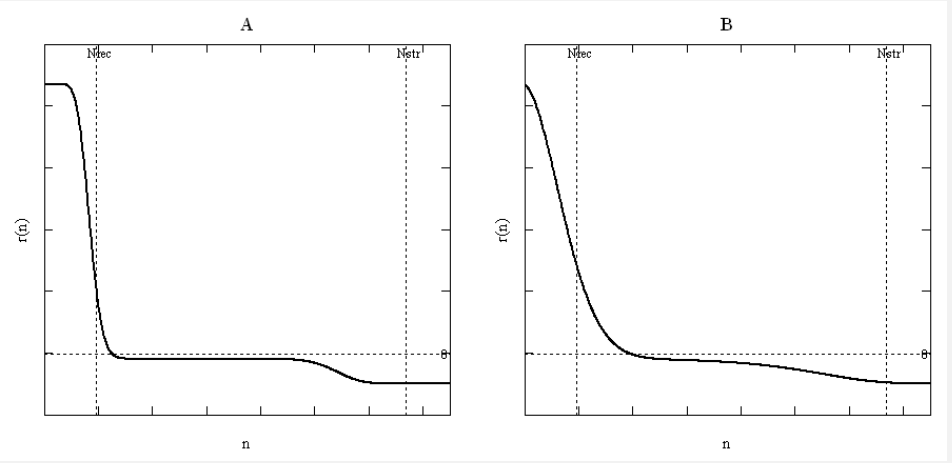

Figure 5| Net growth rate $r(n) = \dot{n}/n$ as function of the shoal size for different values of the level of equality k . (A) Density–dependence of the net growth rate in case of high equality. (B) Density–dependence of the net growth rate in case of high inequality.

This model may be useful for resolving the long-term confusion about density-dependence or the so-called recruitment problem [17]. Firstly, the model clearly shows that density-dependence is a threshold phenomenon. Secondly, the density-dependence is a one-sided (asymmetrical) phenomenon. Equilibrium point $\hat{N}$ is usually located near the recruitment-threshold N_R and thus the density-dependence changes radically depending on the direction in which the shoal size varies. A decrease in size causes a sharp jump in recruitment, whereas the increase in size causes almost no reaction. Thus, it is possible that the population of the time exhibits density-independence, which is then followed by a strong density-dependence. Thirdly, the degree of expression of these thresholds strongly depends on the level of equality in the shoal; in a shoal with high levels of inequality, these thresholds are blurred, and in shoals with a high level of equality, these thresholds are very sharp. Thus, species more involved in shoaling behavior should presumably demonstrate stronger fluctuations in population sizes. Finally, these thresholds are not constant but change with the fluctuations of resources available for the shoal, i.e. thresholds are resource-dependent. This explains why empirical estimations of density-dependence based on statistical analysis of time series give conflicting results: even models that include thresholds, such as for example, a generalized threshold mixed model [19], nevertheless do not take into account the impact of resource changes on the position of these thresholds. Further, we consider the issue of bi-stability no less important to fisheries and associated with the density-dependence.

4. Bi-stability

Analysis of the model shows that bi-stability can occur in populations in two dissimilar cases. First, in the case of very strong effect of hydrodynamic efficiency (4), this may arise for species with larger body size and high speed. Secondly, in the case of strong cannibalism, this may occur in the case of the species forming multi-cohort shoals.

In the first case, we can approximate the density-dependent resource function (2) the following expression

$$R(N) = \frac{R_{\max}}{1 + \lambda(N - N_{opt})^2} \quad , \tag{8}$$

where $R_{\max}$ is maximal resources available for the shoal and λ is parameter that reflects the strength of the hydrodynamic effect. Further substituting (8) into (5) we obtain the equation for the shoal size dynamics, which can have three nontrivial fixed points, two of which are stable (Fig. 6a). One of the points is super-optimal, because it corresponds to the more than optimal size of shoal, while the other is sub-optimal and conforms to the lower shoal size. This suboptimal point is located in the zone of weak density-dependence, while the super-optimal is located in the zone of strong density-dependence. Thus, the differences in the density-dependence can also be directly related to the bi-stability. This point should be emphasized in view of its importance to fisheries. For example, if within a population for a long time there is a strong density-dependence, it may be an early warning signal of possible sharp transition in the sub-optimal state (collapse of fish stocks).

In the second case, we can simulate the effect of cannibalism by adding an extra term in the resource function (2), which reflects the extra amount of resource that the shoal receives from cannibalism. For simplicity, here we are assuming that only the weakest individuals who would have died anyway are consumed, i.e. we consider carrion-cannibalism. This assumption allows us to avoid significant changes in the dynamics model (5). The resource function in the case of carrion-cannibalism can be written

$$\begin{aligned} Rcan(N) &= R(N) + \frac{\gamma}{\sqrt{k}} Surv(N)\left[1 - Surv(N)\right]N^2 \\ Surv(N) &= (1-\delta) I_{\frac{1}{2}}\left(\frac{k\varepsilon_m N}{R(N)} + 1, k\right) \end{aligned} \tag{9}$$

where $Surv(N)$ is the proportion of surviving individuals, γ is a resource value of single prey. The cannibalism rate is assumed to be proportional to the product of the number of potential predators (surviving individuals) and potential prey (dying individuals). This function also takes into account the differences between individuals through the term $1/\sqrt{k}$ (which is a coefficient of variation in a competitiveness distribution), which means that at a high level of equality, cannibalism decreases. Analysis of this model shows that a sufficiently strong cannibalism within the shoal may lead to the emergence of bi-stability (Fig. 6b). Unlike the previous case, where bi-stability occurred at a high level of equality (because of hydrodynamic effects), in this case bi-stability occurs at a high level of inequality (because, at a high level of equality, cannibalism ceases to be possible). As in the first case, here, sub-optimal shoal size shows a weak density-dependence, while the super-optimal shoal size is subject to strong density-dependence.

As the model shows, bi-stability may have fundamentally different causes and consequences depending on the species. In the first case, the cause of bi-stability is the fact that the large shoals, by saving energy on locomotion, are able to explore a large foraging area; respectively, the transition to a sub-optimal state can be expressed in a substantial reduction in the migration area. In the second case, the cause of bi-stability is the fact that

large shoals have more opportunities for cannibalism, and a transition in sub-optimal state respectively results in the reduction of cannibalism.

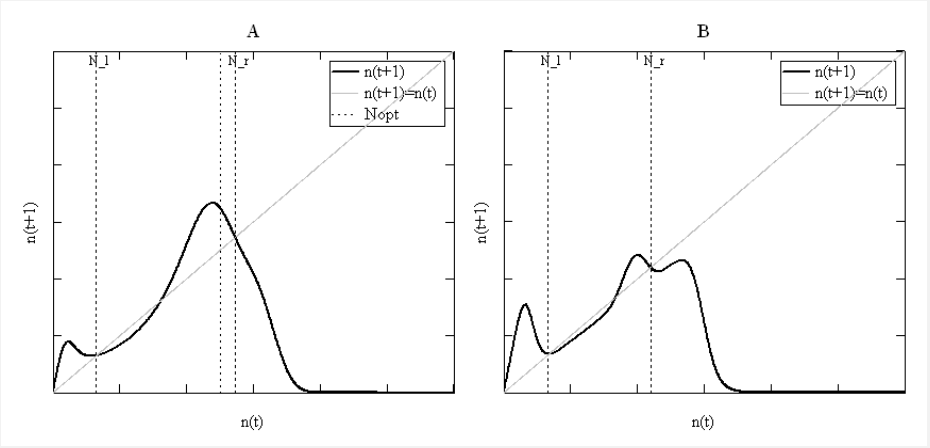

Figure 6| Bi-stability of shoal size: (A) In case of strong hydrodynamic efficiency effect (B) In case of strong cannibalism, N_l and N_r represent the sub-optimal and super-optimal shoal sizes, consequently.

5. Discussion

The shoal-based approach to fish population offers an integrated analytic platform for interdisciplinary studies. We emphasize that further development of fisheries ecology and fish population dynamics cannot be confined only to the improvement of techniques of statistical analysis of time series, but requires co-development of analytical models that are able to take into account explicitly the physiology of fish species, their collective behavior and resources. We also suggest that this shoal-based approach makes the first step in this direction, since it allows for the constructing of species-specific population models that integrate various aspects of biological knowledge about fish behavior and physiology into a unified framework. Unlike other frameworks, this one is to be thought of not so much as a kind of research program, but more as a ready for practical use, analytical tool. We can presuppose that it may find application in several areas.

Firstly, the statistical analysis of empirical data (time series) is definitely in need of such a basic analytical tool, because it provides an opportunity to link data sets such as changes in the overall stock size, changes in resources, changes in the size of shoals, changes in body-size, and changes in migration routes. Thus, such primary questions such as bi-stability and density-dependence can be studied with greater accuracy.

Secondly, a shoal-based mode of management is to be expected. The change of focus from the overall management of the entire stock to the accurate management of shoals seems to promise several advantages, such as a more correct assessment of stock size, accurate accounts of local conditions, and taking into account features of population behavior of different fish species. The model shows that direct estimation of stock size based only on catch data of a few shoals can be significantly biased, because of neglecting the fact that

overall stock consists of shoals. The models as well as empirical studies show that even closely related fish species may have essentially different dynamics. For example, equally large fluctuations in abundance can be quite safe for some species and at the same time lead to the collapse of other species. In this regard, this model can be the basis for an early warning system, since it is able to distinguish between fish species exposed to bi-stability and species that are not exposed to it.

Third, this approach offers a framework for comparative evolutionary studies. For example, it suggests that interplay between physical (hydrodynamic) constrains and evolution may lead to the fact that in the multidimensional trait space (body size, speed, engaging in shoaling behavior and the typical shoal size) fish species should occupy only certain niches. Finally, our study highlights the importance of looking at species shoaling behavior and physiology when analyzing the population dynamics. We have shown how these aspects can affect the density-dependence and bi-stability. In management of fish stock, it is important to have an understanding of these processes. Collectively, the shoal-based approach should improve our analytic understanding of fish populations and may enhance our tools for forecast.

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IV

Epidemiology of conspecific community

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Abstract

This paper introduces an integrated approach to the modeling of epidemics that combines nutrition-dependent physiology and nutrition-dependent immunology of an individual with differences among individuals within a conspecific community. This approach, based on a Conspecific Community Dynamics Model (CCDM), offers a new analytic platform for epidemiological and interdisciplinary studies, which allows for the inclusion into consideration of a greater number of essentially important components. This paper provides significant insight into the crucial role of heterogeneity among individuals in the epidemic process, showing that the inclusion of heterogeneity in the consideration may radically change the whole picture of epidemic dynamics.

Key words: epidemiological models, Conspecific Community Dynamics Models, nutrition-depended physiology, nutrition-depended immunology, epidemic thresholds

1. Introduction

The classical epidemiological modes consider the spread of infections into homogeneous populations, which presumably consist of "average" individuals who are equal in all respects. They also typically ignore the impact of host physical condition and immunocompetence on epidemic dynamics (Beldomenico, P. and Begon , M. 2010). These features of classical models significantly limit their ability to solve many important practical problems. At the same time, more and more empirical studies clearly show that heterogeneity in susceptibility (ref.) and infectiousness (Lloyd-Smith, J.O. et al. 2005), as well as the physical condition of the host (ref.), are actually key factors determining the outbreak of epidemics. Thus, it created a gap between theoretical understanding of the epidemic and results that demonstrate the experiments and observations. In part, this situation can be explained by the fact that there was no clear and simple population model that would explicitly take into account the differences between individuals. However, the newly developed CCDM approach (Sadykov A.M and Stenseth N.C., 2010) offers population models in which inequality between individuals and the resulting inequality in nutrition are explicitly taken into account. The approach is based on nutrition-dependent physiology, which determines the effect of resource acquisition on the life-history of an individual. In this paper, we extend this approach by assuming that individual susceptibility, resilience, infectiousness and loss of immunity also depend on individual resource intake. Thus, the approach allows for the reconsideration of the classical epidemic models in respect of two essential points: heterogeneity among individuals and the underlying physiology of host.

Here we emphasize some details of the CCDM model that will be useful in the design of epidemic models. The classical population models are based on birth-death balance equation, in which overall birth and death rates $\overline{W}(N), \overline{D}(N)$ somehow depend on population size

$$\dot{N} = (\overline{W}(N) - \overline{D}(N))N \tag{1.1}$$

The CCDM approach takes into account the differences in competitiveness among individual within the community and consider overall birth and death rates to be integrals of competitiveness distribution $S(s)$, physiological functions $b(\varepsilon, s), d(\varepsilon, s)$ and stochasticity in the resource distribution $P(\varepsilon \mid s)$

$$\begin{aligned} \overline{W}(N) &= \iint_{0,\infty} b(\varepsilon, s) P(\varepsilon \mid s) S(s) ds d\varepsilon \\ \overline{D}(N) &= \iint_{0,\infty} d(\varepsilon, s) P(\varepsilon \mid s) S(s) ds d\varepsilon \end{aligned} \tag{1.2}$$

where, s and ε are competitiveness and individual resource intake. In turn, a resource distribution function can be calculated as

$$E(\varepsilon, N) = \int_0^\infty P(\varepsilon \mid s) S(s) ds \tag{1.3}$$

The competitiveness distribution represents the differences among individuals within a community in the sense of opportunities to get some share of a common resource. This distribution has shape-scale type $S(s) \equiv S(s \mid k, \theta(R, N))$, where k is independent shape parameter, $\theta(R, N)$ is scale parameter, which depends on population size N and total resource available for the community R. The $P(\varepsilon \mid s)$ represents stochasticity in the resource allocation process, manifested as the difference between expected s and actual ε resource consumption. Various variants of the interplay between competitiveness distribution, stochasticity and resources distribution represent different types of foraging behavior. Physiological functions $b(\varepsilon, s)$ and $d(\varepsilon, s)$ represent the effect of individual competitiveness s and resource intake ε on individual fecundity and mortality. Taking into account the possible disease, we can introduce several physiological functions describing the individual susceptibility $\lambda(\varepsilon, s)$, infectiousness $\mu(\varepsilon', s')$, resilience $\gamma(\varepsilon', s')$ and loss of immunity $\nu(\varepsilon, s)$, where variables with a prime refer to infected individuals. Then, moving from individual physiology to the processes at the community level, we can calculate the following quantities:

$$\begin{aligned} \overline{\mathrm{B}}(N, k) &= \iint_{0,\infty} \iint \lambda(\varepsilon, s) \mu(\varepsilon', s') P(\varepsilon \mid s) P(\varepsilon' \mid s') S(s) S(s') ds ds' d\varepsilon d\varepsilon' \\ \overline{G}(N, k) &= \iint_{0,\infty} \gamma(\varepsilon', s') P(\varepsilon' \mid s') S(s') ds' d\varepsilon' \\ \overline{V}(N, k) &= \iint_{0,\infty} \nu(\varepsilon, s) P(\varepsilon \mid s) S(s) ds d\varepsilon \end{aligned} \tag{1.4}$$

which are direct analogues of such classical epidemiological parameters as transmission, recovery and loss of immunity rates. Note that the transmission rate here is defined by both susceptibility and infectiousness (this double dependence is typically overlooked in classical epidemic models). Further assuming that the infection affects the vital dynamics, we can additionally introduce particular $b(\varepsilon', s'), d(\varepsilon', s')$ fecundity and mortality physiological functions for infected individuals. Thus, we have a full set of variables necessary for modeling various types of epidemics within the community. Such community epidemic

models always take into account differences in host condition and are based on the individual species-specific and pathogen-specific physiology and behavior. The CCDM approach also includes a selection part, and therefore such models, in some degree, can estimate the effect of natural selection. In this particular paper, for illustration purposes, we will use a highly simplified "caricature" version of the general CCDM model, which assumes that: (i) Physiological functions are not directly dependent on the competitiveness and have a very simple one-step dependence on the resource. (ii) The competitiveness distribution is Gamma distribution, the stochasticity distribution is Poisson distribution. (iii) The foraging behavior depends on R/N only. (iv) The infectiousness is constant for all individuals. (v) Pathogen does not evolve and does not select host by conditions other than resource intake. These assumptions allow for the rewriting of the general model in a simpler mathematical form using only certain proportions of individuals instead of distributions.

One-step physiology means that: (i) the individual survives only if it acquired more than ε_m amount of resources. (ii) The individual reproduces only if it acquired more than ε_b ($\varepsilon_b > \varepsilon_m$) resources. (iii) The individual is susceptible to the disease only if it acquired less than ε_β resources and (iv) the individual may recover from the disease only if it acquired more than ε_γ amount of resources. Under such conditions, the birth-death balance equation (1.1) can be rewritten as

$$\dot{N} = [bP_b(\varepsilon_b, N, R, k) - (1-(1-d)P_m(\varepsilon_m, N, R, k))]N \ , \qquad (1.5)$$

where b, d are fecundity and aging mortality rates, $P_b(\varepsilon_b, N, R, k)$ is the proportion of individuals who acquire sufficient resources for survival and reproduction, $P_m(\varepsilon_m, N, R, k)$ is the proportion of individuals who acquire sufficient resources only for survival. These proportions, among others things, depend on the shape parameter $k > 0$, which characterizes the equality of opportunities to obtain resources within the community (further we will mention this value as the equality for short). Small values of k mean a great inequality and therefore very unequal distribution of resources between individuals, large values of k imply greater equality and respectively more uniform distribution of resources. The specific functional forms of these proportions depend on details associated with the collective foraging behavior under resources stochasticity, but these details are not essential for this paper. Further, for the numerical examples we use the following particular functions:

$$\begin{aligned} P_b(\varepsilon_b, N, R, k) &= I_{1/2}\left(\varepsilon_b k \frac{N}{R} + 1, k\right) \\ P_m(\varepsilon_m, N, R, k) &= I_{1/2}\left(\varepsilon_m k \frac{N}{R} + 1, k\right) \end{aligned} \qquad (1.6)$$

where $I_p(x, y)$ is regularized incomplete beta function. These particular functions suggest that the distribution of resources (1.3) among members of the community is a negative binomial distribution, in which the probability of acquiring a certain amount of resources in trial remains constant, while the number of trials required for "success" depends on the size and structure of the community. Using the same resource distribution function, we can also calculate $P_\beta(\varepsilon_\beta, N, R, k)$, the proportion of individuals getting less ε_β resources, and consequently susceptible to disease, as well as $P_\gamma(\varepsilon_\gamma, N, R, k)$, the proportion of individuals capable of recovery.

$$P_\beta(\varepsilon_\beta, N, R, k) = I_{1/2}\left(k, \varepsilon_\beta k\frac{N}{R}+1\right)$$
$$P_\gamma(\varepsilon_\gamma, k, N, R) = I_{1/2}\left(\varepsilon_\gamma k\frac{N}{R}+1, k\right) \quad (1.7)$$

Similarly, you can also calculate the proportion of individuals losing immunity (which may be necessary for the SIRS model).

In this paper, we closely investigate only one particular example of the community-based epidemiological model, which is related to the classical SIS epidemic model without vital dynamics. In this example, we try to demonstrate both the technical aspects of working with community epidemic models, as well as a deeper understanding of the key role of heterogeneity in the spread of infections that these models offer. We also exploit such features of the CCDM model as an explicitness of the resource and investigate an effect of resource variations on epidemic outbreaks. In spite of the wide recognition of the importance of environmental variation as a driving force behind epidemics, the modeling of this force was strongly limited by vague statistical assumptions about possible correlations between the resource and overall epidemic parameters. The CCDM epidemic models allow for the estimating of such effects explicitly and reveal far from trivial aspects of resource-epidemics interactions.

2. The SIS community epidemic model

In general, the SIS conspecific community epidemic model can be written as

$$\dot{X} = \overline{W}(N)X + \overline{W}'(N)Y - \overline{D}(N)X + \overline{G}(N)Y - \overline{B}_i(N)XY$$
$$\dot{Y} = \overline{B}_i(N)XY - (\overline{D}'(N) + \overline{G}(N))Y \quad (2.1)$$
$$\dot{N} = (\overline{W}(N) - \overline{D}(N))X + (\overline{W}'(N) - \overline{D}'(N))Y$$

where $\overline{B}_i(N)$ equals to $\overline{B}(N)$ for a mass action incidence rate or equals to $\overline{B}(N)/N$ for a standard incidence rate. In the absence of vital dynamics (pathogens do not affect the fertility and mortality) $\overline{W}(N) = \overline{W}'(N), \overline{D}(N) = \overline{D}'(N)$ and for "caricature" one-step physiology, the system (2.1) can be rewritten in term of proportions (1.6), (1.7)

$$\dot{X} = bP_b(\varepsilon_b, N/R, k)Y + \gamma P_\gamma(\varepsilon_\gamma, N/R, k)Y - \beta_i P_\beta(\varepsilon_\beta, N/R, k)XY$$
$$\dot{Y} = \beta_i P_\beta(\varepsilon_\beta, N/R, k)XY - ((1-(1-d)P_m(\varepsilon_m, N/R, k) + \gamma P_\gamma(\varepsilon_\gamma, N/R, k))Y \quad (2.2)$$
$$\dot{N} = [bP_b(\varepsilon_b, N/R, k) - (1-(1-d)P_m(\varepsilon_m, N/R, k))]N$$

where β_i equals to β for a mass action incidence or equals to β/N for a standard incidence, β and γ are some positive coefficients. Based on this system we can directly get basic reproductive rates for standard and mass action incidence accordingly:

$$r_{stnd} = \frac{\beta P_\beta(\varepsilon_\beta, \hat{N}/R, k)}{\gamma P_\gamma(\varepsilon_\gamma, \hat{N}/R, k) + bP_b(\varepsilon_b, \hat{N}/R, k)}$$
$$r_{mass} = \frac{\beta P_\beta(\varepsilon_\beta, \hat{N}/R, k)\hat{N}}{\gamma P_\gamma(\varepsilon_\gamma, \hat{N}/R, k) + bP_b(\varepsilon_b, \hat{N}/R, k)} \quad (2.3)$$

where $\hat{N}$ is equilibrium population size. As usual, the value of basic reproductive rates being greater than one means that the infection can spread, and vice versa. In distinction to classical SIS models, here both reproductive rates (2.3) depend on the population size. Therefore, a threshold value of the population size may exist in both cases (in classical SIS model, the

threshold exists only in case of the mass action incidence); moreover, as we show next, two distinctive threshold values may exist.

From this model, we can also get an SI model by the limit $\varepsilon_\gamma \to \infty$, i.e. assuming that the recovery of the individual requires the consumption of unlimited resources and conform to not happening at all. In the SI case, basic reproductive rates turn into

$$\begin{aligned} r_{stnd} &\to \frac{\beta P_\beta(\varepsilon_\beta, \hat{N}/R, k)}{b P_b(\varepsilon_b, \hat{N}/R, k)} \\ r_{mass} &\to \frac{\beta P_\beta(\varepsilon_\beta, \hat{N}/R, k)\hat{N}}{b P_b(\varepsilon_b, \hat{N}/R, k)} \end{aligned} \tag{2.4}$$

again, these rates nontrivially depend on the population size and other parameters.
Now, for comparison with the classical SIS model, we can let $k \to \infty$ and obtain the value of basic reproductive rates in the limiting classical case of a homogeneous population

$$\begin{aligned} \lim_{k\to\infty} r_{stnd}(k) &= \begin{cases} \dfrac{\beta}{\gamma + d} & if \quad \varepsilon_\beta > \varepsilon_b \\ 0 & if \quad \varepsilon_\beta < \varepsilon_b \end{cases} \\ \lim_{k\to\infty} r_{mass}(k) &= \begin{cases} \dfrac{\beta}{\gamma + d}\dfrac{R}{\varepsilon_b} & if \quad \varepsilon_\beta > \varepsilon_b \\ 0 & if \quad \varepsilon_\beta < \varepsilon_b \end{cases} \\ \lim_{k\to\infty} \hat{N}(k) &= \frac{R}{\varepsilon_b} \end{aligned} \tag{2.5}$$

As one would expect, results agree with classical SIS models, when $\varepsilon_\beta > \varepsilon_b$ (indeed it simply means that no one in the population can obtain enough resources to be resistant to the infection and all individuals are equally susceptible), while $\varepsilon_\beta < \varepsilon_b$ means the opposite: that all individuals can procure enough resources to be unsusceptible to the infection. However, results change dramatically if we consider heterogeneity among individuals (finite value of k). The results for SIS community model with the standard incidence and the mass action incidence are summarized in Table 1a and Table 2a accordingly. Apparently, the most prominent feature of these models is that the spread of infection depends critically on the level of equality between individuals, and that this dependence is far from trivial. For instance, under certain conditions (Table 1b and Table 2b), there may be two separate critical thresholds. For example, in Figure 1, we can see the cases in which the epidemic can occur only within certain intermediate range $[k_L; k_R]$ of k . At a high level of inequality (small k), infection does not spread because of a high replacement rate (weak and infected individuals are dying rapidly and do not have enough time to infect others), whereas at a high level of equality (large k) because most individuals are well nourished, and are presumably in good immunological condition (non-susceptible).

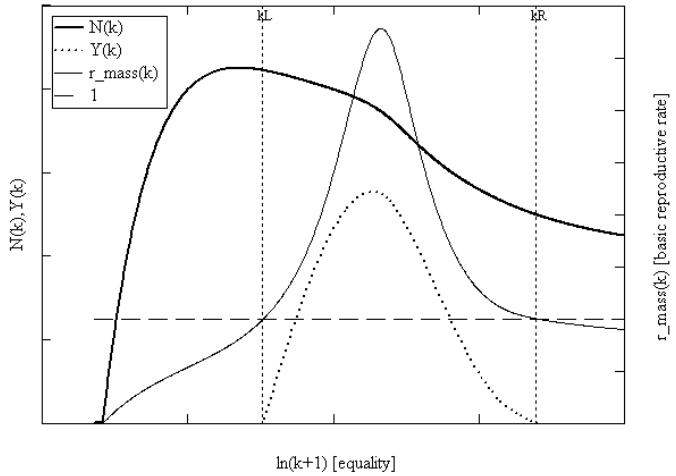

Figure 1| The dependence of population size (bold line), the number of infected (dotted line) and the basic reproductive rate (thin line) from the level of equality between individuals (in case of the mass action incidence). The figure shows the case of two epidemic thresholds k_L and k_R . Epidemics can occur when the basic reproductive rate is higher than one (dash line). This figure shows that, in general, the population size cannot be used for prediction of epidemic outbreaks. In populations with the same size the epidemic can either occur or not occur depending on the equality between individuals in the community.

Note that in models, the value of k in that the population has maximum size does not coincide with the value of k , where the reproductive rate has maximum, i.e. epidemics do not occur because the population size exceeds a certain threshold, but rather from the fact that the population has a certain level of equality. Therefore, the size of the population alone cannot be a reliable predictor of outbreaks if we consider heterogeneity among individuals. On the other hand, the overall condition of the host population measured as the average per individual amount of resources does also not provide unambiguous prediction of epidemic outbreaks (Fig. 2).

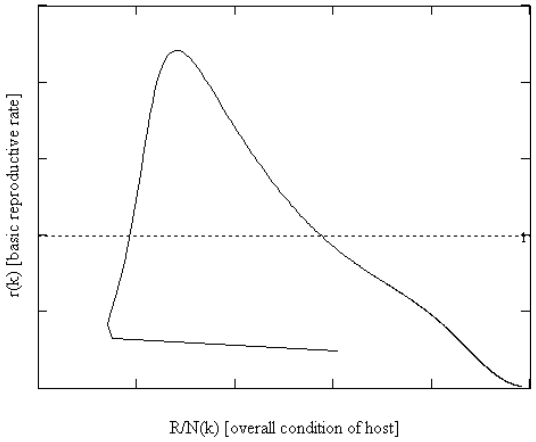

Figure 2| The basic reproductive rate as a function of the overall condition of host population (the average per individual amount of resources) in case of standard incidence. The dotted line is the epidemic threshold. The figure shows that the overall host condition cannot be used for prediction of epidemic outbreaks. Populations with the same overall host conditions can be vulnerable to infection or not at all depending on the level of equality between individuals in the community.

Thus, such traditional characteristics as population size or the average physical condition of individuals cannot be used to predict epidemics properly in cases of heterogeneity. This example demonstrates the importance of such measures of the heterogeneity as the level of equality in the community (the shape parameter of competitiveness distribution), which, in contrast to the other parameters, can give unambiguous values for epidemic thresholds. Indeed, the importance of heterogeneity has been widely recognized in epidemiology (ref.), but in previous studies it has played a supportive role, mainly because its influence on the underlying population dynamics has been ignored. This study demonstrates that the levels of equality and the species-specific physiology are key factors in determining the both population dynamics and epidemiology of the community, while the other parameters are derivative.

3. The effect of resource changes on epidemic outbreaks

In this chapter, we will continue to work with SIS community models introduced earlier, and consider how a change in the resource affects the basic reproductive rate. Here we will consider two different types of resource change: $\dot{R} << \dot{N}$ "slow" changes occur when the community manages to adapt its size to a new equilibrium, and $\dot{R} >> \dot{N}$ the spiky "shock" changes occur when the community does not have time to adapt. It can be shown that for given models the condition $\hat{N} / R = const$ is hold, hence under "slow" resource change, the basic reproductive rate for the standard incidence remains constant $\frac{\partial r_{stnd}}{\partial R} = 0$, while for the mass action incidence it changes proportionally $\frac{\partial r_{mass}}{\partial R} = const$. This is the anticipated result, since the standard incidence assumes the frequency-dependent transmission, while the mass action incidence assumes the density-dependent transmission.

However, in the case of "shock" changes, the situation is not straightforward; in order to evaluate the possible effects needed to calculate the values of derivatives

$$\left.\frac{\partial r_{mass}}{\partial R}\right|_{\hat{N}\equiv const} = \left.\frac{\partial r_{stnd}}{\partial R}\right|_{\hat{N}\equiv const} \hat{N} \qquad (3.1)$$

subject to the constant population size. The values of these derivatives will vary depending on whether birth or mortality rates respond to the resource jump first. Assuming that the sharp change in resource primarily affects survival, we obtain the dependence shown in Figure 3. As we can see, the sign and value of this derivative critically depends on the level of equality. The interesting point here is that, for example, in communities with high levels of inequality, the probability of occurrence of epidemics is reduced in the event of a sharp drop in the resource, whereas in communities with a sufficiently high level of equality, the opposite occurs.

Thus, depending on the level of equality in the community, we can observe a radically different response to the sharp jump in the resource. In the case of a high level of inequality, the decline of the resource leads to increased mortality only among the "malnourished" and more susceptible individuals. As a result, the number of potential spreaders of infection falls and the community becomes more resistant to epidemic outbreaks. In the case of a sufficiently high level of equality, however, the decline of the resource is not so much an increase of deaths from starvation, but more an increase of the proportion of susceptible individuals in the community, and as a result, an increasing number of potential spreaders of infection and thus probability of epidemic outbreaks. In the opposite case of a sharp increase in resources, the

probability of epidemics increases in communities with high levels of inequality, whereas in communities with sufficient high level of equality the opposite occurs.

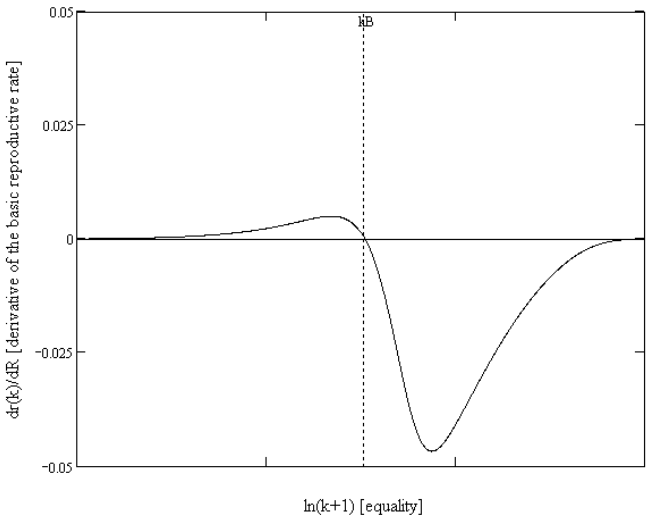

Figure 3| Change of the basic reproductive rate in response to the sharp resource jump for different values of equality among individuals within community. Up to some boundary level of equality $k < kB$, the response is positive, i.e. an increase of the resource leads to increase of the reproductive rate and vice versa. However, for $k > kB$ the response becomes negative i.e. an increase of the resource leads to decrease of the reproductive rate and vice versa.

This example shows that the impact of resource shocks on the outbreak of epidemics in heterogeneous communities cannot be assessed unambiguously without taking into account the level of equality among the members of this community. This point is particularly important given the fact that the long-term effect of the slow change of the resource and the instantaneous effects of resource shocks may also be substantially different. In this situation, the direct use of statistical models to estimate the probabilities of occurrence of epidemics is very problematic, because it not only requires a strict separation of time scales, but also certain criteria explaining the change of sign of the correlations. The approach based on the CCDM models, however, offers the tools to tackle these practical issues.

4. Discussion

In this paper, we considered only one particular example of using the CCDM approach in the field of epidemiology. Nevertheless, even this simple example demonstrates the important implications that an inclusion of heterogeneity among individuals in the host community can have. First, communities that consist of individuals that are unequal in terms of competitiveness, neither the population size nor general physical condition of host can be used for unambiguous prediction of epidemic outbreaks. This conclusion seems very provocative in light of the results that classical epidemiological models suggest, but it is not so. The CCDM approach firstly takes into account the density-dependence in each particular epidemic parameter, and secondly that the very type of density-dependence varies with changes in the level of equality between individuals. Thus, such “non-classical” behavior of the epidemic thresholds is explained by a simultaneous view of both effects.

Second, depending on the time scale and the level of equality in the host community, the resource variation can have a completely different effect on the probability of epidemics. As noted, a sharp drop in resources increases the probability of epidemics in communities consisting of relatively equal individuals, but in communities consisting of unequal individuals, this leads to a decrease in the probability of epidemics. This is relevant, for example, in understanding the impact of environmental changes on the spread of infection, and especially in understanding the seasonality that many infections show.

A third implication concerns natural selection, and particularly how the selection in the host community affects the prevalence of infection. It is well recognized that some pathogens rapidly evolve in order to avoid an adequate response from the immune system of the host, but the role of natural selection in the host community in this process is still not clear. The CCDM models suggest that in a closed (without immigration and emigration) conspecific community, the level of equality is growing under the action of natural selection. Along with the growth of equality the structure of the community is also changing, and thus the proportion of individuals who are unable to provide resources for their reproduction and the maintenance of immunity is constantly decreasing; consequently, pathogens have to deal with an increasingly strong immune response. (Here we consider general strength of immune system of an individual, which is not specific to a certain type pathogen.) As a result, under a certain level of equality (Fig.1) and certain conditions (Tables 1.2), the pathogen could completely disappear from the host population. Depending on the characteristics of pathogens, they can be divided into two basic types: those that are threatened with extinction by natural selection and those that are able to maintain their presence at any level of equality in the community. It is possible to anticipate that the rate of evolution of pathogens in the first type may be higher than the second type. One could also consider the different modes of evolution of a pathogen, such as changes specifically intended to overcome the immune system ($\dot{\varepsilon}_\beta > 0, \dot{\varepsilon}_\gamma > 0$), and some changes aimed at increasing persistence ($\dot{\beta} > 0, \dot{\gamma} < 0$). In general, epidemic CCDM models offer a number of new capabilities for modeling the mutual evolution of pathogen and host immune system, since they are strictly distinguished first and then integrate effects occurring at the level of the individual's immune system and effects occurring at the community level.

We have emphasized that an understanding of epidemic processes in heterogeneous communities requires a paradigm shift from the focus on population size and overall physical condition of host to a focus on the level of equality in the community and underlying species physiology (including immune system), if only because, according CCDM models, the first group of parameters is calculated on the basis of the second group. Of course, it was widely recognized that the heterogeneity should be somehow included in the model of epidemics, but the analysis, surprisingly, reveals that the role of heterogeneity can be so significant as to fundamentally alter the main results of the classical epidemiological models. For example, the SIS model, which in the classical variant could either not have the epidemic threshold (in the case of standard incidence) or have only one threshold value (in case of mass action incidence), with the inclusion of heterogeneity may have a pair of thresholds in both cases.

The approach opens a new way for interdisciplinary integrated research, which allows for incorporating the physiological and immunological studies of an individual with ecological studies of conspecific communities. These researches may provide not only theoretical interest, such as the clarification of fundamental mechanisms behind the host-pathogen interaction under evolutionary and environmental changes, but, more importantly, may be purely practical. For example, they can significantly improve the accuracy of epidemic forecasting by taking into account heterogeneity of immunocompetence among individuals. In view of this, vaccines against many infectious diseases give only a partial

effect that depends on the condition of the individual; such studies can help to design a vaccination program more accurately.

5. Tables

Table 1a| Summary of results for SIS model without vital dynamics and the standard incidence.

Value of k	Value of $r_{stnd}(k)$		Asymptotic behavior of (S,I)	Asymptotic behavior of (X,Y)
$k \to 0$	$r(k) \to \beta$	$\beta < 1$	$(1,0)$	$(0,0)$
		$\beta > 1$	$\left(\frac{1}{\beta}, 1-\frac{1}{\beta}\right)$	$(0,0)$
$0 < k < \infty$	$r(k) < 1$		$(1,0)$	$(\hat{N}(k),0)$
	$r(k) > 1$		$\left(\frac{1}{r(k)}, 1-\frac{1}{r(k)}\right)$	$\left(\frac{\hat{N}(k)}{r(k)}, \hat{N}(k)\left(1-\frac{1}{r(k)}\right)\right)$
$k \to \infty$ $\varepsilon_\beta > \varepsilon_b$ $\varepsilon_\gamma < \varepsilon_b$	$r(k) \to r_\infty$ $r_\infty = \frac{\beta}{\gamma + d}$	$r_\infty > 1$	$\left(\frac{1}{r_\infty}, 1-\frac{1}{r_\infty}\right)$	$\left(\frac{R}{\varepsilon_b r_\infty}, \frac{R}{\varepsilon_b}\left(1-\frac{1}{r_\infty}\right)\right)$
		$r_\infty < 1$	$(1,0)$	$\left(\frac{R}{\varepsilon_b}, 0\right)$
$k \to \infty$ $\varepsilon_\beta > \varepsilon_b$ $\varepsilon_\gamma > \varepsilon_b$	$r(k) \to r_\infty$ $r_\infty = \frac{\beta}{d}$	$r_\infty > 1$	$\left(\frac{1}{r_\infty}, 1-\frac{1}{r_\infty}\right)$	$\left(\frac{R}{\varepsilon_b r_\infty}, \frac{R}{\varepsilon_b}\left(1-\frac{1}{r_\infty}\right)\right)$
		$r_\infty < 1$	$(1,0)$	$\left(\frac{R}{\varepsilon_b}, 0\right)$
$k \to \infty$ $\varepsilon_\beta < \varepsilon_b$	$r(k) \to 0$		$(1,0)$	$\left(\frac{R}{\varepsilon_b}, 0\right)$

Table 1b| The number of epidemic thresholds depending on the conditions for SIS model with the standard incidence.

Conditions				The number of epidemic thresholds
$r_{\max}(k) > 1$	$\beta < 1$	$\varepsilon_\beta > \varepsilon_b$	$r_\infty > 1$	one
			$r_\infty < 1$	two
		$\varepsilon_\beta < \varepsilon_b$		two
	$\beta > 1$	$\varepsilon_\beta > \varepsilon_b$	$r_\infty > 1$	None (constant infection)
			$r_\infty < 1$	two
		$\varepsilon_\beta < \varepsilon_b$		one
$r_{\max}(k) < 1$				None (no infection)

Table 2a| Summary of results for SIS model without vital dynamics and the mass action incidence.

Value of k	Value of $r_{mass}(k)$		Asymptotic behavior of (S,I)	Asymptotic behavior of (X,Y)
$k \to 0$	$r(k) \to 0$		(1,0)	(0,0)
$0 < k < \infty$	$r(k) < 1$		(1,0)	$(\hat{N}(k),0)$
	$r(k) > 1$		$\left(\frac{1}{r(k)}, 1-\frac{1}{r(k)}\right)$	$\left(\frac{\hat{N}(k)}{r(k)}, \hat{N}(k)\left(1-\frac{1}{r(k)}\right)\right)$
$k \to \infty$ $\varepsilon_\beta > \varepsilon_b$ $\varepsilon_\gamma < \varepsilon_b$	$r(k) \to r_\infty$ $r_\infty = \frac{\beta}{\gamma + d}\frac{R}{\varepsilon_b}$	$r_\infty > 1$	$\left(\frac{1}{r_\infty}, 1-\frac{1}{r_\infty}\right)$	$\left(\frac{R}{\varepsilon_b r_\infty}, \frac{R}{\varepsilon_b}\left(1-\frac{1}{r_\infty}\right)\right)$
		$r_\infty < 1$	(1,0)	$\left(\frac{R}{\varepsilon_b}, 0\right)$
$k \to \infty$ $\varepsilon_\beta > \varepsilon_b$ $\varepsilon_\gamma > \varepsilon_b$	$r(k) \to r_\infty$ $r_\infty = \frac{\beta}{d}\frac{R}{\varepsilon_b}$	$r_\infty > 1$	$\left(\frac{1}{r_\infty}, 1-\frac{1}{r_\infty}\right)$	$\left(\frac{R}{\varepsilon_b r_\infty}, \frac{R}{\varepsilon_b}\left(1-\frac{1}{r_\infty}\right)\right)$
		$r_\infty < 1$	(1,0)	$\left(\frac{R}{\varepsilon_b}, 0\right)$
$k \to \infty$ $\varepsilon_\beta < \varepsilon_b$	$r(k) \to 0$		(1,0)	$\left(\frac{R}{\varepsilon_b}, 0\right)$

Table 2b| The number of epidemic thresholds depending on the conditions for SIS model with the mass action incidence.

Conditions			The number of epidemic thresholds
$r_{\max}(k) > 1$	$\varepsilon_\beta > \varepsilon_b$	$r_\infty > 1$	one
		$r_\infty < 1$	two
	$\varepsilon_\beta < \varepsilon_b$		two
$r_{\max}(k) < 1$			None (no infection)

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Modeling the interactions between conspecific communities

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Abstract

This paper expands the Conspecific Community Dynamics (CCD) models on the issue of interaction between communities. In the first part, we consider a model for the standard types of interactions: predator-prey and competition for resources. Particular emphasis is placed on comparing the results of the classical models describing the interaction between species and their counterparts describing the interaction between single-species (conspecific) communities. Then, considering the coexistence of species under resource competition, it is shown that there is a definite relationship between the total number of organisms, the number of coexisting species and the variation between species carrying capacities. In the last part, the paper introduces a model for such type of interaction between communities, which may briefly be described as "warfare", which is a mixture of resource competition and the direct killing of rivals. As an example of such interactions, a model describing the emergence of phytoplankton toxic blooms is considered.

Key words: Ecological community, conspecific community, prey-predator model, Lotka-Volterra competition model, the paradox of the plankton, phytoplankton toxic blooms

1. Introduction

It is generally accepted in ecology that a group of organisms of different species sharing a common environment is not a random collection of individuals, but rather an intrinsically organized (by various interactions) structure or ecological community. However, a similar concept that a group of single-species organisms also provides an example of intrinsically organized structure or conspecific community has developed relatively recently (ref.).
Such an approach assumes that the ecological community does not directly consist of organisms of different species, but rather consists of the other conspecific communities. This paper is based on recently developed models of the dynamics of conspecific community (ref.), and extends these models to the case of interaction between communities. Since these models are based not on the interactions between species, but rather the interactions between conspecific communities, they could equally be used for both intraspecific and interspecific interactions, depending on the context. This paper does not aim to obtain general results, but rather to demonstrate through several examples how the conspecific community model approach tackles basic ecological interactions in comparison with the classical models. Below we briefly recall some features of CCD models that may be useful for further understanding.
The population dynamics part of the conspecific community model represents a simple birth-death balance equation

$$\dot{N} = F_F(N)N = (\overline{W}_F(N) - \overline{D}_F(N))N, \qquad (1.1)$$

where $\overline{W}_F(N), \overline{D}_F(N)$ are overall birth and mortality rates. For simplest one-step physiology functions, which assume that individual dies if it obtains less than ε_m amount of resources and individual reproduces if it obtains more than ε_b amount of resource per unit time, the balance equation can be rewritten as

$$\dot{N} = [(b-c)P_F^b(\varepsilon_b, N, R, k) - (1-(1-\sigma)P_F^m(\varepsilon_m, N, R, k))]N \ , \tag{1.2}$$

where b, c, σ are fecundity, reproduction cost (additional mortality of parents) and aging mortality rates, $P_F^b(\varepsilon_b, N, R, k)$ is the proportion of individuals who acquire sufficient resources for survival and reproduction, $P_F^m(\varepsilon_m, N, R, k)$ is the proportion of individuals who acquire sufficient resources only for survival. These proportions also depend on the total amount available for community resources R and the coefficient k, which characterizes the equality of opportunities to obtain resources among members of the same community. The specific functional forms of these proportions depend on details associated with the collective foraging behavior of members of the community under resources stochasticity, but for this paper, these details are not so important. Further, we assume that these proportions may have the following forms:

$P_F^b(\varepsilon_b, N, R, k) = P_F^b(\varepsilon_b, k, N/R), P_F^m(\varepsilon_m, N, R, k) = P_F^m(\varepsilon_m, k, N/R)$, such choice covers a large number of foraging behavior cases and significantly facilitates comparison of results with the classical models, because it allows one to obtain values that are similar to carrying capacities. In this paper, without loss of generality, for the numerical examples we use the following functions:

$$P_F^b(\varepsilon_b, k, N/R) = I\left(\frac{1}{2}, \varepsilon_b k\frac{N}{R} + 1, k\right), P_F^m(\varepsilon_m, k, N/R) = I\left(\frac{1}{2}, \varepsilon_m k\frac{N}{R} + 1, k\right) \ , \tag{1.3}$$

where $I(p, x, y)$ is regularized incomplete beta function. These particular functions suggest that the distribution of resources among members of the community is a negative binomial distribution, in which the probability of getting a certain amount of resources in trial remains constant, while the number of trials required for "success" depends on the size and structure of the community. A choice of particular type of functions will affect the general results only parametrically; essentially, we will use only the fact that the net growth rate $F_F(N)$ is some function of N/R.

This paper is organized as follows. Section 2 establishes the conspecific community model for prey-predator type of interactions. Section 3 establishes the conspecific community model for resource competition type of interactions. Section 4 then examines pure resource competition. Section 5 introduces a model for resource competition, extermination (warfare) type of interactions between communities. Finally, Section 6 discusses the results and suggests some conclusions.

2. Prey-Predator models

The conspecific community model for prey-predator relation can be written in compact form (hereinafter, for convenience we drop variables that influence the result only parametrically):

$$\begin{aligned} \dot{N} &= F_N(N/R_N)N - P(N,P) \\ \dot{P} &= F_p(P/R_P(N))P \end{aligned} \tag{2.1}$$

where N, P are number of prey and predators, and $F_N(N/R_N)$, $F_p(P/R_P(N))$ are net growth functions that depend on resources R_N, $R_P(N)$ available for prey and predator communities, $P(N,P)$ is a catch function, which can be assumed in the following Holling's like form:

$$P(N,P)=\frac{AN^{2-\chi}P^{\chi}}{1+BN^{2-\chi}} \tag{2.2}$$

where A,B are parameters connected to a search time, attack rate and handling time, χ is coefficient that determines a type of functional response:
$\chi=1,B=0$ Holling's type I, $\chi=1,B\neq 0$ Holling's type II, $\chi<1,B\neq 0$ Holling's type III (Holling, C.S. 1959). Finally, we assume that $R_p(N,P)=\varepsilon_P P(N,P)$, where ε_P is energy content of body of one prey. Isoclines for this system of differential equations (2.1) are

$$\begin{aligned} P&=\left[\frac{F_N(N)(1+BN^{2-\chi})}{AN^{1-\chi}}\right]^{\frac{1}{\chi}} \\ P&=\left[\frac{1+BN^{2-\chi}}{A\varepsilon_P zN^{2-\chi}}\right]^{\frac{1}{\chi-1}} \end{aligned} \tag{2.3}$$

where z is unique nontrivial solution of equation $F_p(z)=0$.
For type I and type II numerical responses, the unique fixed point can be explicitly found

$$\begin{aligned} \hat{N}&=\frac{1}{A\varepsilon_P z-B} \\ \hat{P}&=\frac{1}{A}F_N(\hat{N})(1+B\hat{N}) \end{aligned} \tag{2.4}$$

This point exists if conditions $A\varepsilon_P z>B$ and $\hat{N}<\hat{N}_0$ are holds, otherwise predator population goes to extinction. Here $\hat{N}_0$ is population size of prey in absence of predator. Depending on parameters, the unique fixed point of this system can be stable or cyclic (Fig. 1).

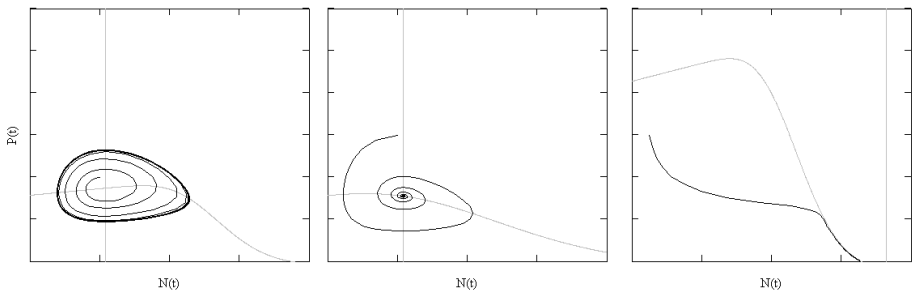

Figure 1 | The isoclines and dynamics of prey-predator system in case of type II numerical response function. The left picture shows standard prey-predator cycle. The central picture shows stable focal point. The right picture shows extinction of predator.

This result does not differ from the result that gives an analogous classical predator-prey model (Kolmogorov, A. 1936). In case of type III numerical response function, there are four generic situations:

(i)Unique fixed stable point exists at small number of prey. (ii) Unique fixed stable point exists at bigger number of prey. (iii) Unique fixed point exists, and is stable or cyclic depending on initial population sizes. (iv) Three fixed points ($(\hat{N}_1, \hat{P}_1), (\hat{N}_2, \hat{P}_2), (\hat{N}_3, \hat{P}_3)$ in order to increase the number of prey) exist and the first and third points are stable, while the second point is always unstable (Fig. 2).

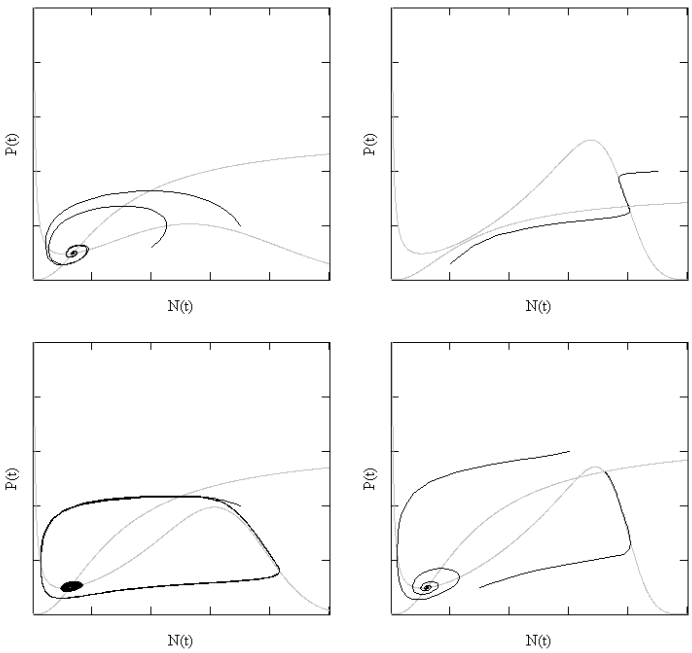

Figure 2 | The isoclines and dynamics of prey-predator system in case of type III numerical response function. Top-left and top-right pictures correspond to case (i) and (ii) consequently. Bottom-left and bottom-right pictures correspond to case (iii) and (iv) (in the paper).

The last two cases may be of interest for applications, since they imply a curious relationship between environmentally and internally driven cycles. For instance, in the third case, depending on the initial conditions, both types of cycles may exist, where the switching from one to another can be a consequence of environmental stochasticity. In the fourth case, environmental stochasticity may lead to switching between two stable points; such a cycle consists of "escaping from predators" and "taking prey under control" sequential processes. In general, the CCD models for predator-prey interactions give similar results to the classical counterparts. However, it should be noted that they potentially have greater precision, as they allow for the inclusion of specific physiological and behavioral details of both communities, as well as the explicit inclusion of resources.

3. Resource competition models

In this chapter, we consider the model of competition for resources between the two conspecific communities. Perhaps the main difference from the classical model is that, in this approach, the resource is presented in an explicit form. For this case, the Conspecific Community Dynamics Model can be written as

$$\dot{X} = F_x(X / R_x(X,Y))X$$
$$\dot{Y} = F_y(Y / R_y(X,Y))Y \qquad (3.1)$$
$$R_x(X,Y) + R_y(X,Y) = R(X,Y)$$

where $R_x(X,Y)$, $R_y(X,Y)$ are resource sharing functions that may have the next generalized form:

$$R_x(X,Y) = \frac{X^\alpha}{X^\alpha + \beta_{xy} Y^\alpha} R$$
$$R_y(X,Y) = \frac{Y^\alpha}{\beta_{yx} X^\alpha + Y^\alpha} R \qquad (3.2)$$

where $\beta_{xy}, \beta_{yx} \geq 0$ represent "degree of influence" of one competitor on resource acquisition of another one, and $\alpha > 0$ is coefficient, which characterizes "strength" of competitors at small population sizes. The meaning of α becomes more clear if we consider a marginal contribution function $M_{xx}(X,Y) = \frac{\partial}{\partial X} R_x(X,Y)$, which reflects how many resources one additional individual can contribute to a "common resource pool". Depending on α there are three different situations: if $\alpha < 1$ then the marginal contribution function monotonically increases up to infinity along with a decrease of the population, if $\alpha = 1$ this function also monotonically increases up to some finite value and if $\alpha > 1$ this function has a maximum at some intermediate point and tends to zero at both big and small population sizes. In other words, $\alpha < 1$ means that at small numbers, the competitor can more easily obtain resources in spite of the presence of much more abundant rivals, or becomes "stronger" at small numbers, $\alpha > 1$ depicts the opposite situation where the competitor becomes "weaker" at small numbers. These three situations can be considered a direct consequence of spatial distribution of individuals: over-dispersed (clamped) distribution (index of dispersion or variance-to-mean ratio $VMR > 1$) suggests large variation of density, therefore an existence of empty patches that can be used as refuge by less abundant competitor, which can be referred to $\alpha < 1$ case. In contrast, under-dispersed (regular) distribution ($VMR < 1$) suggests quite regular density without empty patches, which in turn can be referred to $\alpha > 1$ case. Finally, Poisson distribution ($VMR = 1$) suggests uniform density or well-mixed in space individuals, which can be referred to $\alpha = 1$ case.

We start investigation from case $\alpha = 1$, which can be called "quasi-classic" because it represents a direct analogue of classical competition model (Lotka A.J. 1925) in the sense that it deals with a well-mixed population and gives a similar pair of isoclines. Consequently, four generic situations are possible:

Case A: $\beta_{yx} < \frac{\hat{Y}}{\hat{X}}$ and $\beta_{xy} > \frac{\hat{X}}{\hat{Y}}$, second competitor always wins,

Case B: $\beta_{yx} > \frac{\hat{Y}}{\hat{X}}$ and $\beta_{xy} < \frac{\hat{X}}{\hat{Y}}$, first competitor always wins,

Case C: $\beta_{yx} > \frac{\hat{Y}}{\hat{X}}$ and $\beta_{xy} > \frac{\hat{X}}{\hat{Y}}$, first or second competitor wins, depending on initial conditions,

Case D: $\beta_{yx} < \frac{\hat{Y}}{\hat{X}}$ and $\beta_{xy} < \frac{\hat{X}}{\hat{Y}}$, competitors coexist

where $\hat{X},\hat{Y}$ are equilibrium population sizes in absence of competition, which in turn represents a direct analogue of "carrying capacities". However, in contrast to the classical model, these "carrying capacities" are not arbitrary constants, but functions of physiological and behavioural parameters of each competitor $\hat{X}(b_x,c_x,\sigma_x,\varepsilon_{bx},\varepsilon_{mx},k_x),\hat{Y}(b_y,c_y,\sigma_y,\varepsilon_{by},\varepsilon_{my},k_y)$. This feature allows, if necessary, the tracking down of effects of physiological and behavioural changes on competition outcome. It needs to be pointed out that in this "quasi-classic" case, the total amount of resources obtained by both competitors $R(X,Y)$ does not remain constant and depends on population sizes. In other words, the model explicitly includes additional resource competition effects, which can be either adverse or cooperative. Adverse effect means that some part of available resource is not used by both competitors; this can occur in a situation in which, for instance, the disputed resource does not go to anybody, or when the energy expended in the fight virtually reduces the energy content of the disputed resource. Cooperative effect means that competitors together obtain a greater amount of resources than each of them can obtain separately. The adverse effect corresponds with $\beta_{xy}\beta_{yx}>1$ condition, which leads to $R(X,Y)\le R$ for any X,Y,α. Similarly, the cooperative effect corresponds with $\beta_{xy}\beta_{yx}<1$ condition, and only the unique choice of parameters $\beta_{xy}\beta_{yx}=1$ provides a case of pure resource competition, because only in this case $R(X,Y)=R\equiv const$. It is not a new feature of this particular model; actually, the classic competition model implicitly includes such effects, but gives them another interpretation on what we shall consider later.

It can be shown that for $\alpha=1$:

(i) Pure resource competition yields A and B cases (competitive exclusion) only.

(ii) Presence of additional adverse effect leads to case C (conditional exclusion) only.

(iii)Presence of additional cooperative effect leads to case D (coexistence) only.

Essentially, the quasi-classic model yields the same result as the classic one, but explicitness of resource sharing functions gives a curious interpretation of outcome. Firstly, it suggests that the competition exclusion principle (Gause, G.F. 1932) is a consequence of pure resource competition. Secondly, conditional exclusion is a consequence of resource competition with adverse effect. Finally, competitors can coexist only if they cooperate.

In contrast, the classic interpretation suggests that coexistence is not a product of cooperation, but rather case of competition for two different resources. The distinction here is that our model strictly assumes the competition to be for one resource and explains a surplus amount of resource as a result of cooperation, while the classic one assumes it to be a result of the presence of a second resource. Of course, both interpretations are correct, but they concern different situations, namely the competition for one resource and the competition for two resources. A more striking distinction emerges in relation to adverse effects: the classic interpretation suggests such cases as "pure theoretical", because "an intraspecific competition is always stronger than an interspecific one". In contrast, our model suggests that interspecific and intraspecific competitions are incomparable, since they have a completely different nature. Therefore, conditional exclusion as a product of adverse effect cannot be ruled out from ecological studies, based on an elegant but "pure theoretical" idea of direct comparison of two essentially different types of competition.

This interpretation appears to have several advantages: firstly, it is based on a model that explicitly takes into account the resource. Secondly, it is more consistent, since they do not use the additional implicit assumptions about the second resource, or the relative strength of intraspecific competition, and finally it strictly separates the competition for resources from other aspects of the rivalry.

However, results change dramatically if we consider non-classical ($\alpha \neq 1$) resource sharing functions. A short overview of results can be seen in Table1. Further, we shall concentrate on pure resource competition, having left a theme of interplay between adverse /cooperative effect and α for the next studies.

Table 1 | Results of resource competition for nine different situations

	Competitors becomes "stronger" at small numbers ($\alpha < 1$)	"quasi-classic" case ($\alpha = 1$)	Competitors becomes "weaker" at small numbers ($\alpha > 1$)
Resource competition with adverse effect ($\beta_{xy}\beta_{yx} > 1$, $R(X,Y) < R$)	Coexistence	Conditional exclusion if $\beta_{xy} > 1, \beta_{yx} > 1$ otherwise Competitive exclusion	Conditional exclusion
Pure resource competition ($\beta_{xy}\beta_{yx} = 1, R(X,Y) = R$)	Coexistence	Competitive exclusion	Conditional exclusion
Resource competition with cooperative effect ($\beta_{xy}\beta_{yx} < 1$, $R(X,Y) > R$)	Coexistence	Coexistence if $\beta_{xy} < 1, \beta_{yx} < 1$ otherwise Competitive exclusion	Coexistence or Conditional exclusion

4. Pure resource competition models

In this chapter, we consider the model of pure resource competition between several conspecific communities. Assuming that m is the number of communities competing for one resource, we can write the following system of differential equations, which reflect the dynamics of the system, given the resource constraints

$$\dot{N}_i = F_i(N_i / R_i(N_1,...,N_m))N_i$$

$$R_i(N_1,...,N_m) = \frac{\gamma_i N_i^{\alpha}}{\sum_{i=1}^{m} \gamma_i N_i^{\alpha}} R \qquad (4.1)$$

where γ_i are coefficients, which represent intrinsic ability of $i-th$ community to capture resources.

The isoclines for system (4.1) are

$$\sum_{i=1}^{m} \gamma_i N_i^{\alpha} = \gamma_i N_i^{\alpha-1} K_i \quad , \qquad (4.2)$$

where K_i is the solution of equation $F_i(z/R) \equiv 0$, which represents an equilibrium population size of $i-th$ community in absence of other competitors, which is a direct analogue of "carrying capacity". It can be checked that such a system has at least one nontrivial fixed point, which is stable for $\alpha < 1$. Moreover, for particular value $\alpha = 1/2$, a simple explicit solution can be found:

$$\hat{N}_i = \frac{\gamma_i^2 K_i^2}{\sum_{i=1}^{m} \gamma_i^2 K_i} \qquad (4.3)$$

This result offers a very simple explanation for the paradox of the plankton (Hutchinson, G.E. 1961), because, according to the model, any number of species competing for one resource can

coexist if each of them becomes a stronger competitor with a decrease in population size. As we mentioned above, the property to become a stronger competitor with the lower number is the result of the aggregated spatial distribution, which, in the case of the plankton, is perfectly natural, because of reproduction through cell division. In another way, we can say that reproduction through cell division leads to the fact that newly emerged cells aggregated in the space around the initial cell and this distribution leads to the presence of gaps, which can easily take advantage of numerically smaller competitors. It has been shown (M. Mimura et al. 2000) that the growth of a colony of unicellular organisms can be described by reaction-diffusion equation, which leads to the emergence of multi-fractal spatial structure at low nutrient concentration. These empirically observed structures (E. Ben-Jacob et al. 1994) with many gaps between the branches give an example of how an aggregated spatial distribution can occur in a completely homogeneous environment. Briefly, we can conclude that the ability of plankton species to coexistence is a direct consequence of its unicellular nature and geometry. Here it should be noted that the idea that the spatial distribution may lead to the coexistence of different species and to conform to the solution of the paradox of the plankton was proposed by its author, and has since become dominant in the field of ecology (Chesson, P. 2000). Thus, the explanation of the paradox presented in this paper is not essentially new, but it should be emphasized that it seems to be the simplest version of it, which allows for obtaining explicit analytical solutions even in the case of a large number of interacting communities. The model also offers a number of experimentally verifiable hypotheses: strong mixing as well as the saturation of nutrients should lead to a reduction in the number of coexisting species.

Equation (4.3) also gives a curious relationship between the total number of all organisms, species diversity (variation in the "carrying capacity" between species) and species richness (number of coexisting species).

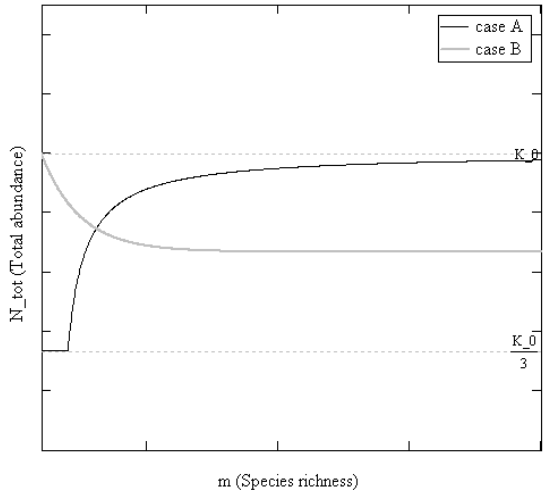

Figure 3 | Relationship between total abundance and species richness in two cases: Case A (black line) represents situation where species with smaller carrying capacity occupy some area first ($K_i = K_0 q^{-i}, i = 0..m, q > 1,$); Case B (solid grey line) represents situation where species with bigger carrying capacity occupy some area first ($K_i = \frac{1}{3} K_0$ for $i = 0..L$ and $K_i = K_0$ for $i = L..m$).

In case of equal ability to capture resources for all competitors ($\gamma_i \equiv 1$), the equation (4.3) for total population size can be rewritten as:

$$\hat{N}_\Sigma = HHI(m,K_i)K_\Sigma = \left(1 - D(m,K_i)\right)K_\Sigma \quad , \tag{4.4}$$

where $\hat{N}_\Sigma = \sum_{i=1}^{m} \hat{N}_i$, $K_\Sigma = \sum_{i=1}^{m} K_i$ and $HHI(m,K_i) = \sum_{i=1}^{m} \left(\frac{K_i}{K_\Sigma}\right)^2$ is the Herfindahl-Hirschman index of domination, which is related to Simpson's diversity index $D(m,K_i)$ (Simpson E.H 1949).

Equation (4.4) also can be rewritten in term of variation $\hat{N}_\Sigma = \left(\frac{1}{m} + m \cdot Var(K,m)\right)K_\Sigma$, where $Var(K,m) = \frac{1}{m}\sum_{i=1}^{m}\left(K_i / K_\Sigma - 1/m\right)^2$.

Equation (4.4) shows that the increase in species richness may have a different impact on the total population size (fig.3). In other words, there is no universal relationship between species richness and total abundance. The effect depends on the order in which species occupy the area. If species with bigger carrying capacity colonize the area first, then the increase in species richness leads to a decrease in the total abundance (Fig.3, case B). Conversely, if species with low carrying capacity inhabit the area first, it leads to an increase in the total abundance (Fig.3, case A). In any case, for a sufficiently large number of coexisting species, this dependence becomes very weak. It can be shown that for randomly and uniformly distributed (within range K_0) carrying capacities $\hat{N}_\Sigma \xrightarrow[m\to\infty]{} \frac{2}{3}K_0$, while in case of geometric progression (fig.3, case B) $\hat{N}_\Sigma \xrightarrow[m\to\infty]{} \frac{q}{q+1}K_0$ (where K_0 is biggest carrying capacity). Thus, the strong dominance of a few species ($q > 2$) gives a great total population size in comparison with a random choice.

Generally, according to equation (4.4) there are two opposite ways that allow for increasing total abundance without changing of species richness: (i) reducing differences between species carrying capacities, and (ii) establishing the strong local dominance of a few species.

5. Resource competition-extermination (warfare) models

In this chapter, we will further exploit the advantages of using the conspecific community model, in the sense that it strictly defines the difference between the capture of resources and actual killing of adversaries, which the classic competition model fails to do.

Here we introduce a model for specific interactions between conspecific communities, which can be called “warfare” and which represents a mixture of resource competition and mutual extermination. Ecological literature includes numerous examples of such interactions; for instance, phytoplankton toxic blooms (G. Pohnert et al. 2007) can be considered one of them.

The resource competition-extermination model can be written as the pure resource competition model with extra terms that represent direct losses of the parties in the case of open conflict.

$$\dot{X} = F_x(R_x(X,Y),X)X - B_x(X,Y)$$
$$\dot{Y} = F_y(R_y(X,Y),X)Y - B_y(X,Y)$$
$$R_x(X,Y) = \frac{X^\alpha}{X^\alpha + \gamma Y^\alpha} R,$$
$$R_y(X,Y) = \frac{\gamma Y^\alpha}{X^\alpha + \gamma Y^\alpha} R \qquad (5.1)$$
$$B_x(X,Y) = IX^{2-\varphi}Y^\varphi,$$
$$B_y(X,Y) = \frac{1}{\nu} IX^\varphi Y^{2-\varphi}$$

Where, $B_x(X,Y), B_y(X,Y)$ are battle casualty functions, I is intensity of conflict, ν is parity of losses, φ is index, which equals to α in case of face-to-face battle or equals to 1 in case of "chemical warfare" in which well-mixed toxin is used. Here we assume pure resource competition in case $\alpha < 1$, which supposes that communities can coexist in the absence of battle, because otherwise we have a trivial case of conditional exclusion reinforced by conflict. The relative strength of rivals has two dimensions and is determined by the ability to capture resources γ, as well as the ability to cause direct loss of the rival population ν (Table 2.). Because of symmetry we need to consider only two possible situations (let Y always has advantage in combat losses ($\nu > 1$)).

Table 2 | Four possible cases of the ratio of advantages, among the conflicting communities

ν	$\gamma < 1, \nu > 1$ X has a comparative advantage in the capture of resources, while Y in the combat losses	$\gamma > 1, \nu > 1$ Y has a comparative advantage in both the capture of resources and combat losses
	$\gamma < 1, \nu < 1$ X has a comparative advantage in both the capture of resources and combat losses	$\gamma > 1, \nu < 1$ Y has a comparative advantage in the capture of resources, while X in the combat losses
	γ	

The model allows one to address some primary questions: Under what conditions can a complete victory (total extermination of one of the contenders) be achieved? Can a limited conflict be "beneficial", i.e. lead to an increase in population size of one of the contenders, and if so under what conditions?

To answer these questions, let us consider the isoclines of the system of the equation.

$$IX^{1-\varphi}Y^{\varphi} = F_x\left(\frac{X^{\alpha}+\gamma Y^{\alpha}}{X^{\alpha-1}}\right)$$
$$IX^{\varphi}Y^{1-\varphi} = \nu F_y\left(\frac{X^{\alpha}+\gamma Y^{\alpha}}{\gamma Y^{\alpha-1}}\right) \quad (5.2)$$

The analysis of these isoclines (in case of $\alpha = 1/2, \varphi = 1$) indicates that:

1. Both isoclines pass through the square $\left[(0,0),\left(\frac{\hat{X}^2}{\hat{X}+\gamma^2\hat{Y}},\frac{\gamma^2\hat{Y}^2}{\hat{X}+\gamma^2\hat{Y}}\right)\right]$, where $\left(\frac{\hat{X}^2}{\hat{X}+\gamma^2\hat{Y}},\frac{\gamma^2\hat{Y}^2}{\hat{X}+\gamma^2\hat{Y}}\right)$ are stable population sizes in absence of conflict.
2. In the biologically meaningful zone ($X > 0, Y > 0$), these isoclines can have none, one, two or three intersections (fixed points).
3. These fixed points can be stable or unstable, and the number of points and their stability strongly depend on value of I (intensity of conflict). For a small value of I only one stable fixed point can exist, while for a sufficiently large value of I only one unstable fixed point can exist.
4. $\dot{X}\left(\frac{\hat{X}^2}{\hat{X}+\gamma^2\hat{Y}}\right) < 0, \dot{Y}\left(\frac{\gamma^2\hat{Y}^2}{\hat{X}+\gamma^2\hat{Y}}\right) < 0$, derivatives at the point of "no conflict" equilibrium are always negative.

Based on this analysis, as well as on the numerical solution of this system (Fig. 4), one can conclude the following: Low intensity conflict is not beneficial for both parties, since it reduces the number of both communities, regardless of the relative strength of each of them. However, with the intensification of the conflict, a community that has advantages in both the capture of resources and combat losses may get some benefits, i.e. to increase its population as compared with before the conflict level. In a further escalation of the conflict, such a community can totally exterminate a rival. In the case where one of the communities has the advantage in combat casualties, and the other to capture resources, the result is determined by the specific ratio of these advantages and much depends on the initial population size of the parties.

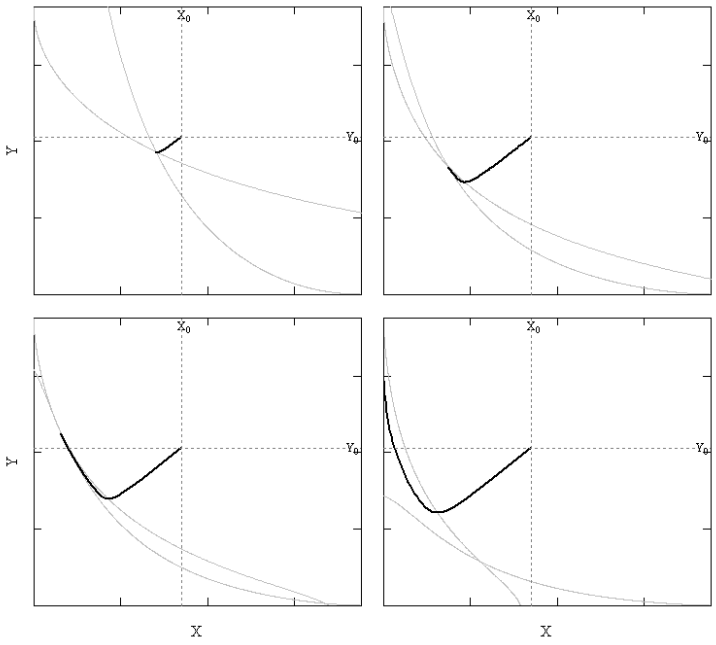

Figure 4 | The isoclines and dynamics of the competition –extermination system in case of four different levels of intensity of conflict. In all cases, the starting point is equal to the number of populations in the lack of open conflict. The top-left picture corresponds to the case of very low intensity conflict, in which there is a decrease in the number of both populations. The top-right picture corresponds to the case of such intensity conflict, in which there is a radical change and the size of one of population begins to increase. The bottom-left picture corresponds to the case of high-intensity conflict, in which one of the populations starts to receive "benefit" from the conflict, i.e. its size becomes greater than that which would have been without conflict. The bottom-right picture corresponds to the case of a very high-intensity conflict, in which one of the populations is completely exterminated.

Among other things, the model offers a mechanism explaining the occurrence of toxic blooms. The principal feature of this mechanism is that it considers the toxicity not as a defense against predators (ref.), but as a special form of resource competition between different phytoplankton species. In other words, this approach explains the toxic bloom as the continuation of resource competition by other means, including "chemical warfare" by the toxin. This explanation seems reasonable, given that phytoplankton is probably more involved in the struggle for resources than in the interactions with predators.

In the case of phytoplankton, the model predicts the occurrence of toxic blooms, in the sense that the process of creation of small and medium levels of toxin does not take advantage, but rather reduces the number of low-toxic species. Thus, one can expect that only highly toxic or non-toxic species may be found, and nothing between. In stable conditions, both groups of species coexist in equilibrium, at which nontoxic species dominate, but a drop in the number of the dominant species can lead to their complete extermination and the emergence of toxic blooms (Fig.5).

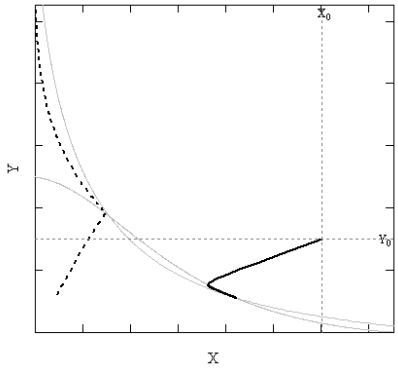

Figure 5 | Emergence of toxic blooms. X, Y are population sizes of nontoxic and highly toxic species respectively. Species may coexist if the initial number of non-toxic species is sufficiently high (solid line). Toxic blooms can occur if the number of dominant nontoxic species suddenly falls (dotted line).

However, it should be emphasized that the decline in the number of non-toxic species can be the result of selective predation (if the toxin also acts on the predator), and, in this sense, the predator may act as a cause of toxic blooms.

6. Discussion

Nutrient acquisition is a major context for ecological interactions among species, but ecologists and nutritionists have thus far developed theory in isolation from each other (Simpson, et al. 2009). In recent years, there have been calls to bridge the divide between the functional study of individual organisms and community ecology with the aim of deriving general principles of community structure, function and evolution from the physiology and behavior of individuals (McGill, B.J. et al. 2007). We suppose that the development in conspecific community-based modeling provides the analytic tool for a new synthesis between species-specific physiology, individual resource acquisition, collective foraging behavior and population dynamics of a conspecific community. Indeed, this paper is only the first step toward an understanding of underlying mechanisms behind the ecological community dynamics and structure. However, even this very first step demonstrates that taking into account differences among individuals and their self-organized nature of necessity leads to the recognition of the important role that conspecific community scale plays. Nonetheless, this "missing" in classical population modeling scale can change a prospective on ecological interaction fundamentally. Firstly, it makes any types of ecological interactions at least two-dimensional, where the interactions of the individual within the conspecific community represent one distinctive dimension, while the interactions outside the individual's own community represent others dimensions. For instance, in case of resource competition, there are two distinctive processes: sharing resources among members of the community and a capture of resources from others communities. We strongly emphasize this difference, because an opposite point of view of necessity leads to neglecting of any kind of self-organization. Secondly, an essential multi-dimensionality leads to extension of basic types of ecological interactions, as we demonstrated through the example of "warfare" relationship, as well as to a new insight on such fundamental issue as species coexistence, as we demonstrated through the example of resource competition. Thirdly, CCD approach without loss of generality considers an ecological relationship in such physiological and behavior details, which, as we suggest, can lead to species-specific population models, where at least each taxa will have own unique analytical population model. Finally, the CCD approach includes a

selection equation, which we do not mention in this paper, but which makes it possible to estimate the effects of selection in each particular case.

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FAQ

What is a main difference between Classical Population Dynamics (CPD) approach and Conspecific Community Dynamics (CCD) approach?

The object of study. CDP deals with a population – an arbitrary collection of some individuals of some kind (not necessarily interacting), while CCD deals with a conspecific community – a self-organized group of diverse interacting individuals. It is possible to say that CCD always includes special intrinsic organizational scale into consideration, while CPD does not. Nevertheless, this "special organizational scale" is self-obvious in biological reality, since it simply represents the fact of existence of such conglomerations as a pack, flock, herd, pride, shoal, swarm, etc., which cannot be considered an arbitrary collection of individuals.

Is the CCD approach a special case of structured resource-customer CPD model applied to the scale of conspecific community?

No, it is not. There are two major reasons for this. First, CPD considers only dynamics of the population size on a single time scale, while CCD mutually considers both dynamics of the population size on "fast" time scale (within generation) and dynamics of an organizational structure on a relatively "slow" time scale (several generations). Thus, in distinction to CPD, CCD includes evolutionary dynamics. Secondly, even in the absence of organizational changes, the dynamics of population sizes are treated differently. CPD evaluates how population size affects average mortality (or survival) and birth rates, while CCD evaluates the physiological response of each individual on certain resource intake. It is possible to say that CPD is an average-based approach, while CCD is a physiology-based approach.

There are many CPD models, which include some intrinsic structure (age, sex, body size or other classes) into consideration. What's so special about CCD?

CPD supposes the population to be structured by some absolute trait (trait that can be measured for each individual independently by comparison with some standard measure of age, mass, length, etc.), while CCD investigates conspecific community structured by a relative trait (trait that can be measured only by comparison of individuals interacting with each other, for example, fitness, competitiveness, social rank, aggressiveness, etc.).

How do particular interactions between individuals lead to the emergence of diversity among individuals (personality) and self sustained organizations?

CCD does not try to answer this question (it falls within the field of studies of Game Theory and IBM). Instead, it simply assumes that such organizations exist as matter of fact (based on extensive biological observations). However, CCD can help to reveal ecological and evolutionary consequences of inequality among individuals.

What is the major difference between the Individual Based Model (IBM) approach and the Conspecific Community Dynamics (CCD) approach?

IBM emphasizes the role of each individual life-history and pairwise interactions, while CCD emphasizes the role of intrinsic organizational structure in connection to the individual as member of the community. In addition, IBM is computer simulation based approach, while CCD is analytical approach.

What are the four most general results that are offered by this approach?

- Population size and stability depend on community structure (i.e. equality among individuals) and this structure can evolve under co-selection (i.e. adaptation of individuals to each other).
- Population is not necessarily limited to the amount of available resources (i.e. equilibrium), but it also possible that population may not have any equilibrium and be limited by co-selection. The latter case supposes that the demographic transition process is not a pure human phenomenon, but rather some consequence of natural selection. Thus, future discovery of demographic transition in wild populations can be anticipated.
- Epidemiological process within conspecific community consisting of individuals that are diverse in terms of immunocompetence critically depends on community structure. In such a case, neither population size nor overall condition of host can be sufficient indicators for epidemic prediction.
- Any number of species competing for one resource can coexist, if each of them becomes a "stronger competitor" at smaller numbers. This "refuge at small numbers" mechanism can be a consequence of a clustered space distribution and gives an evolutionarily stable (i.e. mutations do not reduce diversity) solution for Hutchinson's paradox.